Dynamics on a General Stage Structured n Food Chains

By

© Isam Al-Darabsah

A thesis submitted to the School of Graduate Studies

in partial fulfillment of the requirements for the degree of

Master of Science

Department of Mathematics and Statistics

Memorial University of Newfoundland

August, 2014

St. John's Newfoundland Canada

Abstract

There are many mathematical models to describe the dynamics of plankton community structure in literature, most of the models are based on the so-called prey-predator model. The purpose of this thesis is to propose a general prey-predator model with stage structure and a constant maturation time delay with and without interaction between patches.

First, we begin with the purpose of using delay differential equations in biological models, like those involving population dynamics, epidemiology, and physiology; and present a brief history of the delayed prey-predator models. We provide basic properties of delay differential equations, the Method of Steps to solve them, Chebotarev-Meimans Method and The D-Subdivision Method to determine the local stability.

In Chapter (2), we propose a general model with n parallel food chains through the stage structured maturation time delay, which can cover most of the prey-predator models in the literature. We discuss some basic dynamical properties of the system with single or multiple patches and with general or some particular functional responses, including the existence of equilibrium points and their local and global stabilities.

Then in Chapter (3), based on the model in (2.2), we include the consideration of

migrations between all patches and present a more complex model for the multi-patch predator-prey interactions. We discuss the existence of equilibrium points and their local and global stabilities of the system with two patches and some properties of the general model.

In Chapter (4), we give numerical simulations by choosing some different functions, parameters and time delay in several examples to illustrate the validity of the theoretical results given in Chapter (2) and (3).

At last, in Chapter (5), we summarize the results in this thesis, and indicate some problems for future work.

Dedication

﴿ وَمَا تَوْفِيقِيٓ إِلَّا بِٱللَّهِ ۚ عَلَيْهِ تَوَكَّلْتُ وَإِلَيْهِ أُنِيبُ ﴾

[سورة هود - ٨٨]

I dedicate this work to my parents for their love and sacrifices. To my family and friends, thank you for your encouragement and support.

Acknowledgments

I would like to thank my supervisor Prof. Yuan for her devotion, guidance and support throughout my study. I have been very lucky to have a supervisor who cared so much about my work, and who answered all my questions promptly. Beside my adviser, I would like to thank Prof. Xiaoqiang Zhao and Prof. Chunhua Ou for teaching me dynamical systems and modern perturbation theory courses.

I would also like to thank all staff members at the Department of Mathematics and Statistics, especially Ms. Ros English for her help dealing with travel funds and Mr. Lawrence Greening who provided valuable help with computer problems.

I also want to thank the School of Graduate Studies for the financial support and the Department of Mathematics and Statistics for providing me teaching assistant fellowship.

List of Tables

List of Figures

Contents

Chapter 1

Preliminaries and Intoduction

1.1 Delay Differential Equations in Mathematical Biology

The use of ordinary and partial differential equations to model biological systems has a long history, dating to Lotka and Volterra. As these models are used to understand complicated phenomena, they cannot capture the rich variety of dynamics observed in natural systems. Delay differential equations (DDEs) is one approach to deal with these complexities.

DDEs recently become popular in biological models to represent maturation periods, the birth and death rates, gestation times, incubation periods, transport delays,

feeding times and hunger coefficients in prey-predator interactions, reaction times, food storage or ingestion delays, and resource regeneration times. In disease models, DDEs describe several aspects of infectious disease dynamics: primary infection, drug therapy and immune response. DDEs have also appeared in the study of neural networks, physiology, economics, epidemiology, tumor growth and chemostat models.

In general, DDEs exhibit much more complicated dynamics than ordinary differential equations since the phase space of delay systems is infinite dimensional and a time delay could cause a stable equilibrium to become unstable and cause the populations to fluctuate.

1.2 The Delayed Prey-Predator Models

In ecology, predation explains a biological interaction where a predator feeds on its prey. The prey-predator relationship is essential in maintaining the balance between different animal species. For instance, when there are no predators in an ecosystem, certain species of prey would force other species to extinction as a result of competition.

In the 1920's A. Lotka (1925) and V. Volterra (1926) formulated the orginal model to describe the prey-predator interactions. The LotkaVolterra equations, also known

as the prey-predator equations, are a pair of first-order ordinary differential equations (ODEs)

$$\begin{aligned} \dot{x}(t) &= Ax - Bxy; \\ \dot{y}(t) &= Cy + Dxy, \end{aligned}$$

where x and y are the density of prey and predators, respectively, and A, B, C, $D > 0$. Although there have been many improvements and generalizations on the model using ODEs since then [AG89, Hol59a, Hol59b], the prey-predator interactions include more details. For instance, one can consider a prey-predator model in which the predator population is assumed to have an age structure and use partial differential equations (PDEs) to describe it [CS82] or use DDEs with constant delays and age structure to identify maturity classes [Nun85, DZ13, GK04].

The delayed prey-predator models were first proposed by Volterra in 1928 to study fish population under harvesting. he proposed the equations

$$\begin{aligned} \dot{x}(t) &= x(t)\left(a - bx(t) - \int_{-r}^{0} F_1(\theta)y(t+\theta)d\theta\right); \\ \dot{y}(t) &= y(t)\left(-\delta + cx(t) - \int_{-r}^{0} F_2(\theta)x(t+\theta)d\theta\right), \end{aligned}$$

where x and y are the density of prey and predators, respectively, and all constants and functions are nonnegative [Kua93]. Since then, the prey-predator models with time delay have been studied by several authors, [Kua93] treated both autonomous and nonautonomous systems with various delays and covered the interplay of spatial diffusion and time delays in some diffusive delay population models, [GK04] formulated a general and robust prey-predator model with stage structure with constant maturation time delay and perform a systematic mathematical and computational study, [CN00] established a prey-predator model with stage structure for prey species to obtain the necessary and sufficient condition for the permanence of preypredator and the extinction of one species or two species.

1.3 Basic Properties of Delay Differential Equations

In mathematics, DDEs are differential equation in which the derivative of the unknown functions at present time are dependent on the values of the functions at previous times.

First, define $C = C([s-\tau, s], \mathbb{R})$ and $C^+ = C([s-\tau, s], \mathbb{R}^+)$ with $s \in \mathbb{R}$, $\tau > 0$.

Now, consider the nonlinear DDE

$$\dot{x}(t) = f(x(t), x(t-\tau)) \tag{1.1}$$

with a single delay $\tau > 0$. For the initial value problem, we need to give an initial function or initial history from C, i.e a solution $x(t)$ of (1.1) satisfy

$$x(t) = \phi(t), \ \ s - \tau \leq t \leq s. \tag{1.2}$$

Theorem 1.1. *([Smi10] - Theorem 3.1 on page 26) Let $f(t, x, y)$ and $f_x(t, x, y)$ be continuous on $\mathbb{R}^3$, $s \in \mathbb{R}$, and $\phi : [s - \tau, s] \to \mathbb{R}$ be continuous. Then there exists $\delta > 0$ and a unique solution of the initial-value problem (1.1)-(1.2) on $[s - \tau, s + \delta]$.*

Theorem 1.2. *([Smi95] - Theorem 5.2.1 on page 81) Let $D \subset C$ is open. Assume that whenever $\phi \in D$ satisfies $\phi \geq 0$, $\phi_i(0) = 0$ for some i and $t \in \mathbb{R}$, then $f_i(t, \phi) \geq 0$. If $\phi \in D$ satisfies $\phi \geq 0$ and $t_0 \in \mathbb{R}$, then $x(t, t_0, \phi) \geq 0$ for all $t > t_0$ in its maximal interval of existence.*

The Method of Steps is one of several methods used for solving DDE system, this method allows to solve any DDE system by transforming it to an ODE system over a particular interval, by using the known history function for that interval. Then,

the process is repeated in the next interval with the newly found solution working as the history function for the next interval.

For example, Consider the initial value problem

$$\begin{cases} x'(t) = \alpha x(t) - \beta x(t-\tau), t \geq 0 \\ \quad x(t) = \phi_0(t), -\tau \leq t \leq 0, \end{cases}$$

where $\tau > 0$ is fixed, and assume that $\phi_0(t)$ is continuous on $[-\tau, 0]$. Then we obtain

- When $-\tau \leq t \leq 0$, $x(t) = \phi_0(t)$.

- When $0 \leq t \leq \tau$, $x'(t) = \alpha x(t) - \beta\phi_0(t-\tau),\ t \in [0,\tau] \quad x(0) = \phi_0(0)$

  $\Longrightarrow x(t) = \phi_0(0) + \int_0^t [\alpha x(s) - \beta\phi_0(s-\tau)]ds := \phi_1(t).$

- When $\tau \leq t \leq 2\tau$, $x'(t) = \alpha x(t) - \beta\phi_1(t-\tau),\ t \in [\tau, 2\tau] \quad x(0) = \phi_1(\tau)$

  $\Longrightarrow x(t) = \phi_1(\tau) + \int_\tau^t [\alpha x(s) - \beta\phi_1(s-\tau)]ds := \phi_2(t).$

And so on, we can continue this process.

Local stability of DDE equilibrium point is determined by the location of roots of of the characteristic equation which has a transcendental form

$$\Delta(\lambda) = P(\lambda) + Q(\lambda)e^{-\lambda\tau} = 0$$

where $P(\lambda)$ and $Q(\lambda)$ are polynomial in λ. Generally, this equation has infinitely many solutions. There are many methods available to determine the local stability. For instance, **Chebotarev-Meiman's Method** which is a generalization of the Routh-Hurwitz criteria [CM49]. To apply the method, First, we take an infinite series expansion of the characteristic function

$$D_1(z) = \sum_{k=0}^{\infty} a_k z^k.$$

Then, we rewrite $D_1(i\omega)$ as $u(\omega) + iv(\omega)$ with

$$u(\omega) = \sum_{k=0}^{\infty} (-1)^k a_{2k} z^{2k}, \quad v(\omega) = \sum_{k=0}^{\infty} (-1)^k a_{2k+1} z^{2k+1}.$$

Next, we define determinants, as in the Routh-Hurwitz criteria,

$$Q_1 = a_1,\ Q_2 = \begin{vmatrix} a_1 & a_3 \\ a_0 & a_2 \end{vmatrix}, \cdots,\ Q_m = \begin{vmatrix} a_1 & a_3 & a_5 & \cdots & a_{2m-1} \\ a_0 & a_2 & a_4 & \cdots & a_{2m-2} \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & \cdots & a_m \end{vmatrix}$$

Finally, we have the following theorem.

Theorem 1.3. *Assume that $u(\omega)$ and $v(\omega)$ have no common zeros. Then the quasi-polynomial D_1 is stable if and only if $Q_m > 0$ for all $m \in \mathbb{N}_0$.*

The D-Subdivision Method is another method to study the local stability, this method consists of computing a particular decomposition of the parameter space in regions such that the number of characteristic roots with positive real parts is constant with respect to all the points of the parameter space inside the region, and such that for each point of the boundaries the corresponding characteristic equation has at least one root on the imaginary axis [MN07].

Chapter 2

Dynamics on a General Stage Structured n Parallel Food Chains

2.1 Introduction

Plankton are the productive base of both marine and freshwater ecosystems, they divided into functional groups: Phytoplankton, plant, the first link in the food chain and known as primary producers because they produce the first forms of food; Zooplankton, animal, the intermediate link that transfers energy captured by phytoplankton to fish and other animals near the top of the food chain. Moreover, they produce oxygen through phytoplankton which removes carbon dioxide from seawater and allows the

water to absorb a lot of carbon dioxide produced in the atmosphere. The structure of the ecosystem has their population, growth, mortality, distribution and diversity. Simultaneously, a changing environment effects their dynamics [KB12].

There are many mathematical models to describe the dynamics of plankton community structure in literature, we refer [Col80, EB96, EY00, CZ11, OY09, LK08, ML02] and the references cited there. Most of the models are based on the so-called prey-predator model.

Armstrong [Arm99] studied a model structure with n parallel food chains, each consisting of a phytoplankton species P_i and its dedicated zooplankton predator Z_i, proposed the following system

$$\begin{aligned} P_i' &= P_i\left[\mu_i(N) - Z_i h_i(P_i)\right] \\ Z_i' &= Z_i\left[\gamma_i P_i h_i(P_i) - \epsilon_i\left(\sum_{j=1}^{n} Z_j\right)\right], \end{aligned} \tag{2.1}$$

for $i = 1, \ldots, n$ and $N = T - \sum_{i=1}^{n} P_i - \sum_{i=1}^{n} Z_i$, with the growth rate $\mu_i(N)$ of P_i which is a function of nutrient concentration N, the per-phytoplankton-per-zooplankton harvest rate $h_i(P_i)$ of P_i by Z_i, predation on the zooplankton $\epsilon_i\left(\sum_{j=1}^{n} Z_j\right)$ by higher trophic levels. The constant parameter T is the nutrient supply, γ_i is the growth efficiency of Z_i. The diagram Fig. (2.1) shows the structure of three parallel food

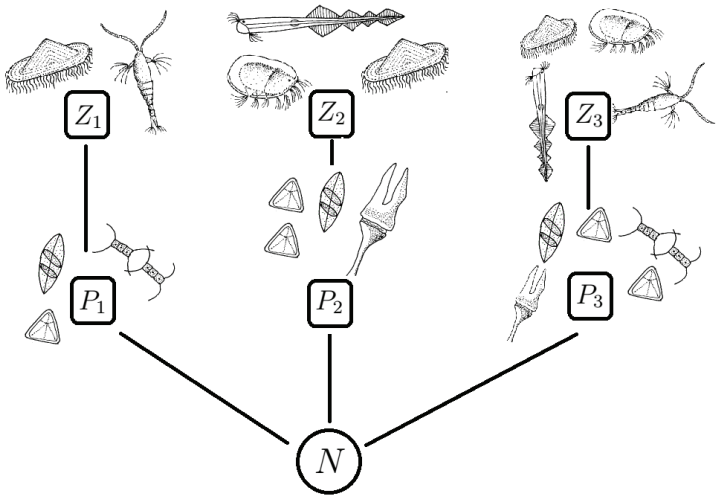


Figure 2.1: Three parallel food chains.

chains.

2.2 The model

Gourley and Kuang pointed out in [GK04], in reality, the growth of species is a combined result of birth and death processes, which is closely linked to the resource supply. The authors in [GK04] formulated a general prey-predator model with stage structure with constant maturation time delay. Adopting the idea of stage structure, we modify the model (2.1) to the following:

$$\begin{aligned}\frac{dP_i}{dt} &= P_i[\mu_i(\mathcal{N}) - Z_i h_i(P_i)],\\ \frac{dZ_i}{dt} &= b_i e^{-d_i\tau_i} P_i(t-\tau_i) Z_i(t-\tau_i) h_i(P_i(t-\tau_i)) - Z_i\epsilon_i\left(\sum_{k=1}^{n} Z_k\right),\end{aligned} \tag{2.2}$$

where $\mathcal{N} = T - \sum_{k=1}^{n} \alpha_k P_k - \sum_{k=1}^{n} \beta_k Z_k$ is the nutrient concentration with the coefficients $\alpha_k, \beta_k, (k = 1, \cdots, n)$ related to the efficiency of nutrient consuming for each species. We assume that, only the adult predators are capable of preying on the prey species, so Z_i is the adult zooplankton taxon feeding on the phytoplankton P_i, b_i denotes the adult predator's birth rate, d_i is the mortality death rate of the juvenile (through-stage death rate), τ_i is the unit of time to mature. We omit the equation of juvenile since it is decoupled. All the parameters are positive.

From the view points in biology and analysis, we assume that all the functions $\mu_i(\mathcal{N}), h_i(P_i)$ and $\epsilon_i(\sum_{k=1}^{n} Z_k)$ are continuous and differentiable, and satisfy the following hypothesis for $i = 1, \ldots, n$:

(C_1) $\mu_i(0) = 0$, $\frac{d\mu_i}{d\mathcal{N}} > 0$ when $\mathcal{N} \in [0, T]$;

(C_2) $h_i(P_i) \geq 0$, $\frac{d(P_i h_i(P_i))}{dP_i} > 0$, $0 \leq P_i h_i(P_i) \leq M_i$, M_i is a constant;

(C_3) $\frac{\partial \epsilon_i(Z)}{\partial Z_j} \geq 0$ for each Z_j in $Z = \sum_{k=1}^{n} Z_k$.

The general model (2.2) can cover almost all the prey-predator models in the literature, such as the well known Lotka-Volterra model and Rosenzweig-MacArthur model. In addition, (2.2) includes several general, partial general and specific models with some particular choices of the functions. For example, when $n = 1$, with $\mu(\mathcal{N}) = g(P), h(P) = \frac{p(P)}{P}, \epsilon(Z) = d$(constant) and $\tau = 0$, (2.2) becomes the general model in [KR08]; with $\mu(\mathcal{N}) = r(1-P(t)/K), h(P) = \frac{p(P)}{P}, \tau \neq 0$ and constant $\epsilon(Z) = d_j$, (2.2) covers the partial general model in [GK04]; when we take $\mu(\mathcal{N}) = R(1-P(t)/K)$ and the Holling type II and III functional responses $h(P) = \frac{A}{C_1+P(t)}, \epsilon(Z) = d + \frac{FZ(t)}{C_2^2+Z(t)^2}$, τ is either zero or nonzero, the model (2.2) is the same as that in [Yua12]. When $n \geq 2$, the two-patch predator-prey models in [RH11] without migration or the n-patch ecological model [HH08] without dispersal are involved in our model (2.2) as well.

2.3 One Phytoplankton and One Zooplankton Model

We start with the simplest case when $n = 1$ which is rewritten as

$$\begin{aligned} \frac{dP}{dt} &= P[\mu(\mathcal{N}) - Zh(P)], \\ \frac{dZ}{dt} &= be^{-d\tau}P(t-\tau)Z(t-\tau)h(P(t-\tau)) - Z\epsilon(Z), \end{aligned} \tag{2.3}$$

with $\mathcal{N} = T - \alpha P - \beta Z$.

The purpose of this section is to analyze and demonstrate the population dynamics of various species in model (2.3) by finding the ultimate upper bound for the interacting populations and exploring the local stability of the all the equilibrium solutions.

Let $C = C([-\tau, 0), R)$, $C^+ = C([-\tau, 0), R^+)$, first, we have the following positivity and boundedness properties.

Theorem 2.1. *Given the initial condition $P(0), Z(0) \in C^+$, then under the hypothesis (C_1 - C_3), the solutions of (2.3) are nonnegative in $X = C \times C$. In addition, if $\epsilon(0) > 0$ then all the solutions are ultimately bounded in X.*

Proof. The positivity for $P(t)$ is just followed by standard arguments from the first equation in (2.3) since it contains a factor of $P(t)$.

For $Z(t)$, on $0 \leq t \leq \tau$, $Z'(t) \geq -Z\epsilon(Z)$, so $Z(t) \geq Z(0)\ e^{-\int_0^t \epsilon(Z(s))ds} > 0$. By using step-method, we have $Z(t) > 0$ for all $t \in [0, \infty)$. Therefore the solutions of (2.3) are nonnegative in X.

Under the hypothesis (C_1), $\mu(\mathcal{N})$ is increasing function with respect to $\mathcal{N}$, then

$$P' = P[\mu(\mathcal{N}) - Zh(P)] \leq P\mu(\mathcal{N}) \leq P\mu(T - \alpha P).$$

Since $\mu(0) = 0$ and $\mu(T-\alpha P)$ is decreasing with respect to P, we know $\limsup_{t\to\infty} P(t) \leq T/\alpha := \mathcal{T}$, implying $P(t)$ is ultimately bounded.

From the hypothesis (C_3), $\epsilon(Z) \geq 0$ for all $Z \geq 0$, multiplying the first equation by $be^{-d\tau}$ and adding it to the second equation in (2.3), we can obtain

$$\begin{aligned}\left(be^{-d\tau}P(t) + Z(t+\tau)\right)' &= be^{-d\tau}P(t)\mu\left(\mathcal{N}\right) - \epsilon(Z(t+\tau))Z(t+\tau) \\ &\leq be^{-d\tau}\mu(T)P(t) - \epsilon(0)Z(t+\tau),\end{aligned}$$

which is equivalent to

$$\begin{aligned}\left(be^{-d\tau}P(t) + Z(t+\tau)\right)' &\leq be^{-d\tau}\mu(T)P(t) + be^{-d\tau}\epsilon(0)P(t) - \epsilon(0)\left(be^{-d\tau}P(t) + Z(t+\tau)\right) \\ &\leq b\mathcal{T}e^{-d\tau}\left(\mu(T) + \epsilon(0)\right) - \epsilon(0)\left(be^{-d\tau}P(t) + Z(t+\tau)\right).\end{aligned}$$

If $\epsilon(0) > 0$ then $\limsup_{t\to\infty}\left(be^{-d\tau}P(t) + Z(t+\tau)\right) \leq \frac{b\mathcal{T}e^{-d\tau}(\mu(T)+\epsilon(0))}{\epsilon(0)}$. Therefore, both $P(t)$ and $Z(t)$ are ultimately bounded in X. □

- **Existence and Stability of Boundary Equilibrium Points**

It is easy to see that in the system (2.3), there is a trivial equilibrium point $(0, 0)$ and one-species equilibrium point $(\frac{T}{\alpha}, 0) := (\mathcal{T}, 0)$. The stability of these two boundary equilibrium points are given in the following result.

Theorem 2.2.

(i) $(0,0)$ *is always an unstable saddle point;*

(ii) $(\mathcal{T},0)$ *is locally asymptotically stable if* $\epsilon(0) > b\mathcal{T}h(\mathcal{T})e^{-\tau d}$ *and it is unstable if* $\epsilon(0) < b\mathcal{T}h(\mathcal{T})e^{-\tau d}$.

Proof. **(i)** The linearization of (2.3) at $(0,0)$ is

$$\begin{aligned} x'(t) &= \mu(T)x(t) \\ y'(t) &= -\epsilon(0)y(t). \end{aligned}$$

So it is easy to see that $(0,0)$ is a unstable saddle point since $\mu(T) > 0$ and $\epsilon(0) > 0$.

(ii) The linearization of (2.3) at $(\mathcal{T},0)$ is

$$\begin{aligned} x'(t) &= -\mathcal{T}[\alpha\mu'(0)x(t) + (\beta\mu'(0) + h(\mathcal{T}))\, y(t)], \\ y'(t) &= -\epsilon(0)y(t) + be^{-d\tau}\mathcal{T}h(\mathcal{T})y(t-\tau). \end{aligned} \tag{2.4}$$

The characteristic equation of (2.4) is

$$\Xi(\lambda) = (\lambda + \alpha\mathcal{T}\mu'(0))\left(\lambda + \epsilon(0) - b\mathcal{T}h(\mathcal{T})e^{-\tau(\lambda+d)}\right) = 0.$$

Let $f(\lambda) = \lambda + \epsilon(0) - b\mathcal{T}h(\mathcal{T})e^{-\tau(\lambda+d)}$. Since $f(0) = \epsilon(0) - b\mathcal{T}h(\mathcal{T})e^{-\tau d}$, if $\epsilon(0) <$

$b\mathcal{T}h(\mathcal{T})e^{-\tau d}$, then $f(0) < 0$ and $\lim_{\lambda\to+\infty} f(\lambda) = +\infty$. Therefore there exist $\bar{\lambda} > 0$ such that $f(\bar{\lambda}) = 0$, thus $(\mathcal{T}, 0)$ is unstable.

When $\epsilon(0) > b\mathcal{T}h(\mathcal{T})e^{-\tau d}$, assume there exists a zero of $f(\lambda)$ with $Re(\lambda) > 0$, then from

$$Re\lambda = Re(b\mathcal{T}h(\mathcal{T})e^{-\tau(\lambda+d)} - \epsilon(0)) \leq b\mathcal{T}h(\mathcal{T})e^{-\tau d} - \epsilon(0) < 0,$$

which leads to a contradiction. Therefore all the eigenvalues in (2.4) have negative real parts, implying $(\mathcal{T}, 0)$ is locally asymptotically stable. □

In order to study the persistence of system (2.3), assume that X is the closure of open set X°; that is, $X = X^\circ \cup \partial X^\circ$, where ∂X°, assumed to be nonempty, is the boundary of X°. Also, we assume that the $C^\circ -$ semigroup $T(t)$ on X satisfies

$$T(t) : X^\circ \to X^\circ, \quad T(t) : \partial X^\circ \to \partial X^\circ \tag{2.5}$$

Denote $T_\partial(t) = T(t)|_{\partial X^\circ}$ and A_∂ be the global attractor for $T_\partial(t)$.

Theorem 2.3 ([Kua93], Page 277, Theorem 2.4)**.** *Suppose that $T(t)$ satisfies (2.5) and that*

(i) *there is a $t_0 > 0$ such that $T(t)$ is compact for $t > t_0$; and*

(ii) *$T(t)$ is point dissipative in X ; and*

(iii) *$\tilde{A}_\partial = \underset{x\in A_\partial}{\cup} \omega(x)$ is isolated and has an acyclic covering $M = \{M_1, M_2, \ldots, M_n\}$.*

Then $T(t)$ is uniformly persistent if and only if, for each M_i, $W^s(M_i) \cap X^\circ = \phi$ where $W^s(M_i) = \{x : x \in X, \omega(x) \neq \phi, \omega(x) \subset M_i\}$.

Theorem 2.4 ([Kua93], Page 277, Theorem 2.3)**.** *Suppose that $T(t)$ satisfies (2.5) and that*

(i) *there is a $t_0 > 0$ such that $T(t)$ is compact for $t > t_0$; and*

(ii) *$T(t)$ is point dissipative in X ; and*

(iii) *$T(t)$ is uniformly persistent.*

Then there is a global attractor $A_\circ$ in X° relative to strongly bounded sets.

Theorem 2.5. *If $\epsilon(0) < b\mathcal{T}h(\mathcal{T})e^{-\tau d}$, then system (2.3) exhibits uniform persistence.*

Proof. First, we define

$$\begin{aligned} X_1 &= \left\{(P, Z) \in R^2 : P \geq 0, Z = 0\right\}; \\ X_2 &= \left\{(P, Z) \in R^2 : P = 0, Z > 0\right\}; \\ \partial X^\circ &= X_1 \cup X_2; \\ X^\circ &= \left\{(P, Z) \in R^2 : P > 0, Z > 0\right\}. \end{aligned}$$

From Theorem 2.1, we can see that $X = X^\circ \cup \partial X^\circ$ is positively invariant.

We denote $(P(t), Z(t)) = (P(t, \varphi, \psi), Z(t, \varphi, \psi))$ the solution of system (2.3) with $(P_0, Z_0) = (\varphi, \psi)$. Hence,

$$T(t)(\varphi, \psi)(\theta) = (P(t + \theta, \varphi, \psi), Z(t + \theta, \varphi, \psi)), \ \theta \in [-\tau, 0].$$

Then, according to ([Kua93], Theorem 2.8, page 20), $T(t)$ is completely continuous for $t > \tau$. Also, Theorem 2.1 implies that $T(t)$ is point dissipative. Therefore, conditions (i) and (ii) of Theorem 2.3 are satisfied.

There are two steady states in ∂X°: $E_0 = (0, 0)$ and $E_1 = (\mathcal{T}, 0)$. We know from Theorem 2.2-(i) that E_0 is unstable saddle point and the Jacobian matrix has two eigenvalues $\lambda_1 = \mu(T) > 0$ and $\lambda_2 = -c < 0$. The positive eigenvalue λ_1 corresponds to an eigenvector of the form $(1, 0)^T$. The negative eigenvalue λ_2 corresponds to an eigenvector of the form $(0, 1)^T$, and hence corresponding to solutions that remain in the part of ∂X°. Thus, the stable manifold of E_0 does not intersect the X°, that is, $W^s(E_0) \cap X^\circ = \phi$. When $\epsilon(0) < b\mathcal{T}h(\mathcal{T})e^{-\tau d}$, E_1 is unstable, Theorem 2.2-(ii). There is a unique positive eigenvalue $\bar{\lambda} > 0$, which corresponds to an eigenvector of the form $(\frac{\bar{\lambda} + \mathcal{T}\alpha\mathcal{T}\mu'(0)}{\mathcal{T}(\beta\mu'(0) + h(\mathcal{T})}, 1)^T$. The negative eigenvalue $-\alpha\mathcal{T}\mu'(0)$ corresponds to an eigenvector of the form $(1, 0)^T$ and all roots with a negative part of $\lambda + \epsilon(0) - b\mathcal{T}h(\mathcal{T})e^{-\tau(\lambda+d)} = 0$

correspond to an eigenvector of the form $(0,0)^T$, hence corresponding to solutions that remain in the part of ∂X°. Thus, the stable set of E_1 does not intersect the X°, that is, $W^s(E_1) \cap X^\circ = \phi$.

To verify the condition (iii) of Theorem 2.3, let $\tilde{A}_\partial$ be the union of the two steady states E_0 and E_1. Taking M_i to be these steady states, there are no cycles in the ∂X°. Also, these steady states are isolated invariant set by the linear theory ([Kua93], Section 2.8). Hence, by Theorem 2.3, system (2.3) is uniformly persistent. □

To discuss the global attractivity of the equilibrium point $(\mathcal{T}, 0)$, we introduce the result given in [GK04, Kua93]:

Lemma 2.1. *Consider the following equation*

$$u'(t) = au(t-\tau) - bu(t)$$

where $a, b, \tau > 0$, *and* $u(t) > 0$ *for* $-\tau \leq t \leq 0$. *We have*

(i) $\lim_{t\to\infty} u(t) = 0$, *when* $a < b$;

(ii) $\lim_{t\to\infty} u(t) = \infty$, *When* $a > b$.

Then we have the following:

Theorem 2.6. *With the hypothesis (C_1 - C_3). When $bMe^{-d\tau} < \epsilon(0)$ then the solutions of (2.3) satisfy $P(t) \longrightarrow \mathcal{T}, Z(t) \longrightarrow 0$ as $t \longrightarrow \infty$.*

Proof. In the proof of Theorem (2.1), we know that $\limsup_{t\to\infty} P(t) \leq \mathcal{T}$. Therefore there exists $t_\delta > 0$ such that

$$P(t) < \mathcal{T} + \delta, \quad \text{for all } t \geq t_\delta.$$

Following the hypothesis (C_2) and (C_3), we have $\epsilon(Z) \geq \epsilon(0)$ and $P(t-\tau)h(P(t-\tau)) \leq M$ for any $t > t_\delta + \tau$ with positive constant M. Thus

$$\begin{aligned} Z' &\leq bMe^{-d\tau} Z(t-\tau) - \epsilon(Z) Z(t) \\ &\leq bMe^{-d\tau} Z(t-\tau) - \epsilon(0) Z(t). \end{aligned}$$

The comparison theory implies that $Z(t)$ is bounded above by the solution of

$$u'(t) = bMe^{-d\tau} u(t-\tau) - \epsilon(0) u(t), \quad t > t_\delta + \tau$$

such that $u(t) = Z(t)$ for $t \in [t_\delta, t_\delta + \tau]$. The condition $bMe^{-d\tau} < \epsilon(0)$ and the result in *Lemma(2.1)* guarantee $\lim_{t\to\infty} Z(t) = 0$.

Let $\eta \in (0,1)$ such that $T - \eta(\beta + M) > 0$. Then there exists $t_\eta > 0$ such that for

$t \geq t_\eta$, $Z(t) < \eta < \frac{T}{\beta+M}$. By the boundedness of $Ph(P)$, we have $PZh(P) < M\eta$.

Therefore

$$\begin{aligned} P' &= P\mu(\mathcal{N}) - Ph(P)Z > P\mu(\mathcal{N}) - M\eta \\ &= P\mu(T - \alpha P - \beta Z) - M\eta > P\mu(T - \alpha P - \beta\eta) - M\eta. \end{aligned}$$

In general, $T - \alpha P(t) \geq T - \alpha \limsup_{t\to\infty} P(t) \geq 0$. Thus

$$P' \geq P\mu(T - \alpha P - \beta\eta) - M\eta - (T - \alpha P - \eta(\beta + M)).$$

That the equation

$$v'(t) = v(t)\mu(T - \alpha v(t) - \beta\eta) - M\eta - (T - \alpha v(t) - \eta(\beta + M))$$

has a solution $v(t) = \frac{T-\beta\eta}{\alpha}$ results $\liminf_{t\to\infty} P(t) > \frac{T-\beta\eta}{\alpha}$. Since $\eta \in \left(0, \frac{T}{\beta+M}\right)$ is arbitrary, $\liminf_{t\to\infty} P(t) \geq \frac{T}{\alpha} = \mathcal{T}$. Together with $\limsup_{t\to\infty} P(t) \leq \mathcal{T}$, we have $\lim_{t\to\infty} P(t) = \mathcal{T}$. □

Since $Ph(P)$ is bounded by M, we can see the condition for the local stability at $(\mathcal{T}, 0)$ in Theorem (2.2)-(ii) is included in the global stability condition in Theorem (2.6).

- **Existence and Stability of Positive Equilibrium**

When system (2.3) has a positive equilibrium point (P^*, Z^*), then P^*, Z^* must satisfy

$$\begin{aligned} \mu(\mathcal{N}^*) &= Z^* h(P^*), \\ be^{-d\tau} P^* h(P^*) &= \epsilon(Z^*), \end{aligned} \tag{2.6}$$

with $\mathcal{N}^* = T - \alpha P^* - \beta Z^*$. From the second equation in (2.6), we have

$$\frac{\epsilon(Z^*)e^{d\tau}}{b} = P^* h(P^*) \leq M. \tag{2.7}$$

Since $\epsilon(0) \leq \epsilon(Z^*)$, (2.7) implies that τ must be less than $\tau_{\max} = \frac{1}{d} \ln\left(\frac{bM}{\epsilon(0)}\right)$. The condition $\tau < \tau_{max}$ is necessary for the existence of such P^* and Z^* in (2.6), but is not a sufficient condition in general.

In addition, the existence of such P^*, Z^* and the number of solutions in (2.6) are uncertain which depends on the choice of the functions $\mu(\mathcal{N}), h(P)$ and $\epsilon(Z)$. For instance, in Fig. (2.2), $f(P) = Ph(P)$ and $g(Z) = \frac{\epsilon(Z)e^{d\tau}}{b}$, the second equation of

(2.6) may have infinite solutions (Fig. (2.2a)) or none solution (Fig. (2.2b)). Let

$$\tilde{\tau} = \sup\{\tau \in (0, \tau_{\max}) \,|\text{the second equation of (2.6) has at least a solution}\}. \quad (2.8)$$

When $\tau < \tilde{\tau}$, mathematically, we can obtain

$$Z^* = \epsilon^{-1}(be^{-d\tau}P^*h(P^*)),$$

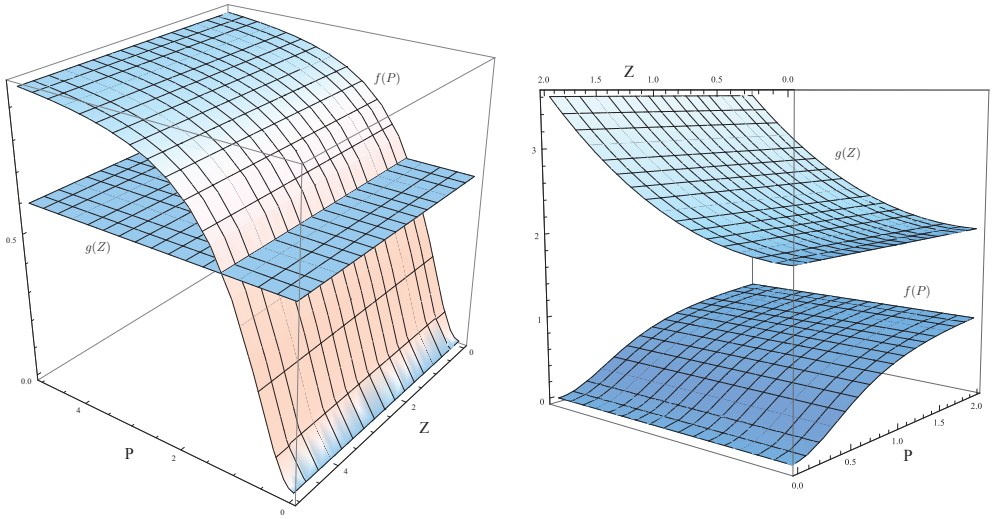
while P^* is determined by

$$\mu(T - \alpha P^* - \beta\epsilon^{-1}(be^{-d\tau}P^*h(P^*))) = h(P^*)\epsilon^{-1}(be^{-d\tau}P^*h(P^*)),$$

which is impossible to find an analytical solution in general. However, when the total higher trophic predation $\epsilon(Z)$ is a constant, then the positive equilibrium point (P^*, Z^*) exists and is unique.

Theorem 2.7. *When $\epsilon(Z) = c$ is a constant and $bMe^{-d\tau} > c$, there exists a unique positive equilibrium point (P^*, Z^*) in (2.3).*

Proof. When $\epsilon(Z) = c$, $g(Z) = \frac{\epsilon(Z)e^{d\tau}}{b} = \frac{ce^{d\tau}}{b} = \hat{c}$ is a constant with fixed parameters b, c, d and τ. Since $f(P) = Ph(P)$ is a increasing function on the interval $(0, \mathcal{T})$ with $0 < f(P) \leq M$, when $M > \hat{c}$, that is, $bMe^{-d\tau} > c$, there exists a unique $P^* \in (0, \mathcal{T})$



(a) $\epsilon(Z) = 0.15,\ h(P) = \frac{P}{P^2+1}$. (b) $\epsilon(Z) = 0.5 + 0.1Z^2,\ h(P) = \frac{P}{P^2+0.5}$.

Figure 2.2: The existence of solution in the second equation of (2.6). $b = 0.25$, $d = 0.01$, $\tau = 0.2$, and $T = 9$.

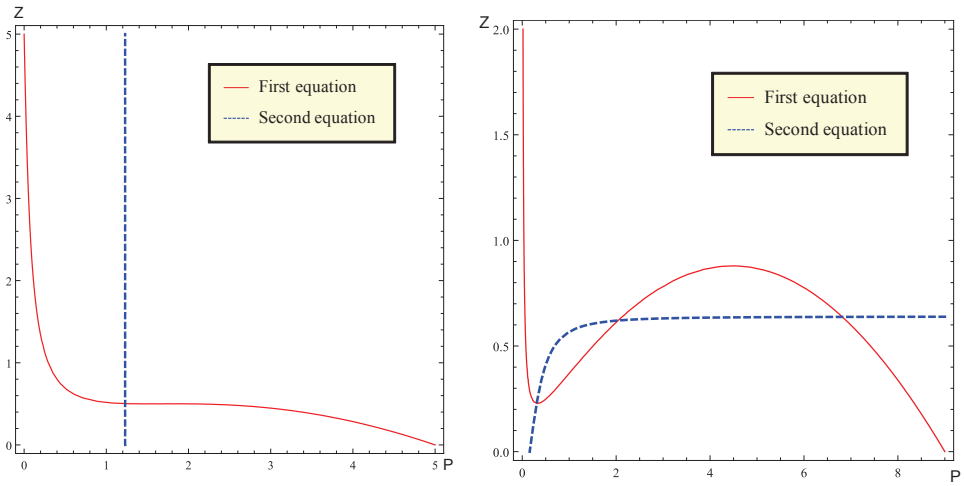
such that $f(P^*) = g(Z^*) = \hat{c}$, i.e $P^* = f^{-1}(\hat{c})$.

In Eq. (2.6), multiplying Z^* in the second and combine with the first equation, we have $be^{-d\tau}P^*\mu(N^*) = Z^*\epsilon(Z^*) = cZ^*$, that is

$$be^{-d\tau}f^{-1}(\hat{c})\mu(T - \alpha f^{-1}(\hat{c}) - \beta Z^*) = cZ^*. \tag{2.9}$$

In Eq. (2.9), the left-hand side is decreasing, and the right-hand side is increasing with respect to Z^*, thus there exists a unique Z^* corresponding to $P^* = f^{-1}(\hat{c})$, implying the system (2.6) has a unique positive equilibrium point (P^*, Z^*). □

With fixed parameters, feasible values of delay τ and certain functions given in



(a) One equilibrium point. (b) Three equilibrium points.

Figure 2.3: Existence of (P^*, Z^*) with $b = 0.25, d = 0.01, \alpha = \beta = 1$ and functions in table (2.1).

Table (2.1), Fig. (2.3) shows the existence of (P^*, Z^*). When $\epsilon(Z)$ is a constant, there is a unique positive equilibrium point shown in Fig.(2.3a), while when we change ϵ from a constant to a linear function, we can observe three positive equilibrium points, see Fig.(2.3b).

	$h(P)$	$\mu(N)$	$\epsilon(Z)$	T
Fig. (2.3a)	$\frac{P}{P^2+1}$	$\frac{N}{N+10}$	0.15	5
Fig. (2.3b)	$\frac{P}{P^2+0.1}$	$\frac{N}{N+15}$	$0.05 + 0.31Z$	9

Table 2.1: Functions chosen in Fig. (2.3).
$\alpha = \beta = 1$

When the positive equilibrium point (P^*, Z^*) exists, to study its stability, we

linearize (2.3) at (P^*, Z^*), by setting $x = P - P^*, y = Z - Z^*$, which is,

$$\begin{aligned} \frac{dx}{dt} &= -P^*(\alpha\mu'_* + Z^*h'_*)x(t) - P^*(\beta\mu'_* + h_*)y(t), \\ \frac{dy}{dt} &= -(\epsilon_* + Z^*\epsilon'_*)y(t) + be^{-d\tau}Z^*(h_* + P^*h'_*)x(t-\tau) + be^{-d\tau}P^*h_*y(t-\tau), \end{aligned} \tag{2.10}$$

where h_*, ϵ_* denotes the value of the function h, ϵ and $\mu'_*, h'_*, \epsilon'_*$ denotes the value of the derivative of the associated function at (P^*, Z^*) respectively. The characteristic equation of (2.10) is

$$\Delta(\lambda, \tau) = \lambda^2 + a_1\lambda + a_2 + b_1\lambda e^{-\tau\lambda} + b_2e^{-\tau\lambda} = 0, \tag{2.11}$$

with

$$\begin{aligned} a_1 &= P^*(\alpha\mu'_* + Z^*h'_*) + (\epsilon_* + Z^*\epsilon'_*), \\ a_2 &= P^*(\beta\mu'_* + Z^*h'_*)(\epsilon_* + Z^*\epsilon'_*), \\ b_1 &= -be^{-d\tau}P^*h_* < 0, \\ b_2 &= -be^{-d\tau}(P^*)^2h_*(\alpha\mu'_* + Z^*h'_*) + be^{-d\tau}Z^*P^*(\beta\mu'_* + h_*)(h_* + P^*h'_*). \end{aligned}$$

As we know that all the roots of $\Delta(\lambda, \tau)$ with $Re(\lambda) \geq 0$ lie in a bounded domain

[DZ13]. When $\tau = 0$. Eq. (2.11) becomes

$$\Delta(\lambda, 0) = \lambda^2 + (a_1 + b_1)\lambda + (a_2 + b_2) = 0,$$

where

$$\begin{aligned} a_1 + b_1 &= P^*(\alpha\mu'_* + Z^*h'_*) + Z^*\epsilon'_*, \\ a_2 + b_2 &= P^*(\alpha\mu'_* + Z^*h'_*)Z^*\epsilon'_* + be^{-d\tau}P^*Z^*(\beta\mu'_* + h_*)(h_* + P^*h'_*) \\ &= P^*(\alpha\mu'_* + Z^*h'_*)Z^*\epsilon'_* + be^{-d\tau}P^*Z^*(\beta\mu'_* + h_*)\left.\frac{dPh}{dP}\right|_{P=P^*}. \end{aligned}$$

$a_1 + b_1 > 0$ if and only if $h'_* > -\left(\frac{\alpha\mu'_*}{Z^*} + \frac{\epsilon'_*}{P^*}\right)$ and since $\frac{dPh}{dP} > 0$, we have $a_2 + b_2 > 0$ if and only if $h'_* > \frac{-be^{-d\tau}}{Z^*\epsilon'_*}(\beta\mu'_* + h_*)(\left.\frac{dPh}{dP}\right|_{P=P^*}) - \frac{\alpha\mu'_*}{Z^*}$. Following the Routh-Hurwitz stability criterion we have

Proposition 2.1. *At $\tau = 0$, the equilibrium point (P^*, Z^*) is locally asymptotically stable if and only if*

$$h'_* > -\left(R + \frac{\mu'_*}{Z^*}\right), \tag{$\mathbf{H_0}$}$$

where $R = \min\left\{\frac{\epsilon'_*}{P^*}, \frac{be^{-d\tau}}{Z^*\epsilon'_*}(\beta\mu'_* + h_*)(\left.\frac{dPh}{dP}\right|_{P=P^*})\right\}$.

Let $\tau > 0$ and suppose $\lambda = i\omega$ $(\omega > 0)$ is a purely imaginary root of (2.11).

Substituting it into (2.11) and separating the real and imaginary parts, we obtain:

$$\begin{aligned} -\omega^2 + a_2 &= -b_1\omega \sin\omega\tau - b_2 \cos\omega\tau \\ a_1\omega &= -b_1\omega \cos\omega\tau + b_2 \sin\omega\tau. \end{aligned} \tag{2.12}$$

Squaring and adding both equations of (2.12) lead to

$$F(\omega, \tau) = \omega^4 + q(\tau)\omega^2 + \ell(\tau) = 0,$$

where

$$\begin{aligned} q(\tau) &= a_1^2 - 2a_2 - b_1^2, \\ \ell(\tau) &= a_2^2 - b_2^2. \end{aligned}$$

Let $u = \omega^2$. In seeking of the positive real roots in $F(u, \tau) = u^2 + q(\tau)u + \ell(\tau) = 0$, at first we need

$$\Theta = q(\tau)^2 - 4\ell(\tau) = \left(a_1^2 - b_1^2\right)\left(a_1^2 - b_1^2 - 4a_2\right) + 4b_2^2 \geq 0. \tag{$\mathbf{H_1}$}$$

Obviously, $F(u, \tau) = 0$ has no positive roots when $\ell(\tau) \geq 0$ and $q(\tau) \geq 0$ which is

equivalent to

$$a_2^2 - b_2^2 \geq 0 \quad \& \quad a_1^2 - 2a_2 - b_1^2 \geq 0; \tag{$\mathbf{H_2}$}$$

and has exactly one positive root if

$$\ell(\tau) = a_2^2 - b_2^2 < 0; \tag{$\mathbf{H_3}$}$$

or when

$$\ell(\tau) = a_2^2 - b_2^2 = 0 \quad \& \quad q(\tau) = a_1^2 - 2a_2 - b_1^2 < 0; \tag{$\mathbf{H_4}$}$$

or two positive roots when $\ell(\tau) > 0$ and $q(\tau) < 0$ which is equivalent to

$$a_2^2 - b_2^2 > 0 \quad \& \quad a_1^2 - 2a_2 - b_1^2 < 0. \tag{$\mathbf{H_5}$}$$

Furthermore, from (2.12), we have

$$\begin{aligned} \sin \omega(\tau)\tau &= \frac{a_1 b_2 \omega(\tau) - b_1 \omega(\tau)\left(a_2 - \omega(\tau)^2\right)}{b_1^2 \omega(\tau)^2 + b_2^2}, \\ \cos \omega(\tau)\tau &= \frac{b_2\left(\omega(\tau)^2 - a_2\right) - a_1 b_1 \omega(\tau)^2}{b_1^2 \omega(\tau)^2 + b_2^2}. \end{aligned} \tag{2.13}$$

Define the function $\theta(\tau) \in [0, 2\pi)$ such that $\sin\theta(\tau)$ and $\cos\theta(\tau)$ are given by (2.13).

Following [BK02], [LS10], let

$$S_n(\tau) = \tau - \frac{\theta(\tau) + 2n\pi}{\omega(\tau)}, \quad n \in \mathbb{N}, \quad \tau \in (0, \tau_{\max}), \tag{2.14}$$

then $i\omega(\tau^*)$ is a root in (2.11) if and only if τ^* is a zero of a function S_n for some $n \in \mathbb{N}$.

Proposition 2.2. *If $\tau^* \in (0, \tau_{\max})$ is a positive root of S_n given in (2.14) for some $n \in \mathbb{N}$, then a pair of purely imaginary roots $\omega(\tau^*)$ of (2.11) exist which crosses the imaginary axis from left to right if $S_n'(\tau^*) > 0$ and crosses the imaginary axis from right to left if $S_n'(\tau^*) < 0$, and*

$$Sign\left\{\frac{d\mathrm{Re}(\lambda)}{d\tau}\bigg|_{\lambda=i\omega(\tau^*)}\right\} = Sign\left\{\frac{dS_n(\tau)}{d\tau}\bigg|_{\tau=\tau^*}\right\}.$$

Therefore, when the positive equilibrium point (P^*, Z^*) exists, the stability of (P^*, Z^*) is given in the following:

Theorem 2.8. *(i) When ($\boldsymbol{H_0}$), ($\boldsymbol{H_1}$) and ($\boldsymbol{H_2}$) hold, (P^*, Z^*) is locally asymptotically stable for any feasible time delay τ;*

(ii) When ($\boldsymbol{H_0}$), ($\boldsymbol{H_1}$) with either ($\boldsymbol{H_3}$), ($\boldsymbol{H_4}$) or ($\boldsymbol{H_5}$) hold, (P^*, Z^*) is locally asymptotically stable for small time delay τ, say $\tau < \min\{\tau_n^*\}$;

(iii) When ($\boldsymbol{H_0}$) *does not hold and* ($\boldsymbol{H_1}$) *with either* ($\boldsymbol{H_3}$), ($\boldsymbol{H_4}$) *or* ($\boldsymbol{H_5}$) *hold,* (P^*, Z^*) *is unstable for small time delay* τ. *If there exists a* τ_n^*, *such that* $S_n'(\tau_n^*) < 0$, (P^*, Z^*) *can become stable with* $\tau > \tau_n^*$.

From Theorem 2.4 and Theorem 2.5, we have

Proposition 2.3. *If* $\epsilon(Z) = c$ *is a constant and* $b\mathcal{T}h(\mathcal{T})e^{-\tau d} > c$, *then the positive equilibrium point* (P^*, Z^*) *of system (2.3) is global attractive when* (P^*, Z^*) *is locally asymptotically stable.*

2.4 n Parallel Phytoplankton Zooplankton Patches

In this section, we discuss the general model (2.2) with n parallel phytoplankton-zooplankton patches. Rewrite the system (2.2) as

$$\begin{aligned}
P_1{}' &= P_1\left[\mu_1(\mathcal{N}) - Z_1 h_1(P_1)\right] \\
Z_1{}' &= b_1 e^{-d_1\tau_1} P_1(t-\tau_1) Z_1(t-\tau_1) h_1(P_1(t-\tau_1)) - Z_1\epsilon_1\Big(\sum_{k=1}^{n} Z_k\Big) \\
&\vdots \\
P_n{}' &= P_n[\mu_n(\mathcal{N}) - Z_n h_n(P_n)] \\
Z_n{}' &= b_n e^{-d_n\tau_n} P_n(t-\tau_n) Z_n(t-\tau_n) h_n(P_n(t-\tau_n)) - Z_n\epsilon_n\Big(\sum_{k=1}^{n} Z_k\Big).
\end{aligned} \tag{2.15}$$

Analogue to the positivity and boundedness property given in Theorem (2.1), we have the following result.

Theorem 2.9. *Given the initial condition $P_i(0), Z_i(0) \in C^+$, for all $i = 1, \ldots, n$, then under the hypothesis (C_1 - C_3), the solutions of (2.15) are nonnegative in $\mathcal{X} = C^n \times C^n$. In addition, if each $\epsilon_i(0) > 0$, then the solutions are ultimately bounded in $\mathcal{X}$.*

The proof of Theorem (2.9) is similar to that in Theorem (2.1) , we omit here.

System (2.15) has a trivial equilibrium point $E_0 = \underbrace{(0, 0, \ldots, 0, 0)}_{2n}$ and infinite number of predator-free equilibrium points, and it is also possible to have the co-existed positive equilibrium point $(P_1^*, Z_1^*, P_2^*, Z_2^* \ldots, P_n^*, Z_n^*)$ under the hypothesis (C_1 - C_3) and certain conditions.

Remark 2.1. *System (2.15) has infinite number of predator-free equilibrium points with the form $\tilde{E} = \underbrace{\left(\alpha_1 \tilde{P}_1, 0, \alpha_2 \tilde{P}_2, 0, \ldots, \alpha_n \tilde{P}_n, 0\right)}_{2n}$ such that $\sum_{k=1}^{n} \alpha_k \tilde{P}_k = T$.*

To study the stability of any equilibrium point (x_1,y_1,x_2,y_2, ... ,x_n,y_n), we need to know the general form of the characteristic equation, which is,

$$\Delta(\lambda) = \det\left(\lambda I - J^0 - \sum_{k=1}^{n} J^k e^{-\lambda \tau_k}\right) = 0$$

where $J^0 = (a_{ij})$ and $J^k = \left(c_{ij}^k\right)$ are $2n \times 2n$ matrices with

$$a_{ij} = \begin{cases} -x_{\frac{i+1}{2}}\left[\alpha_{\frac{i+1}{2}}\mu'_{\frac{i+1}{2}}\left(\bar{\mathcal{N}}\right) + y_{\frac{i+1}{2}}h'_{\frac{i+1}{2}}\left(x_{\frac{i+1}{2}}\right)\right] & , \quad i \text{ odd}, j = i; \\ -x_{\frac{i+1}{2}}\left[\beta_{\frac{i+1}{2}}\mu'_{\frac{i+1}{2}}\left(\bar{\mathcal{N}}\right) + h_{\frac{i+1}{2}}\left(x_{\frac{i+1}{2}}\right)\right] & , \quad i \text{ odd}, \ j = i+1; \\ -\alpha_{\frac{j+1}{2}}x_{\frac{i+1}{2}}\mu'_{\frac{i+1}{2}}\left(\bar{\mathcal{N}}\right) & , \quad i, j \text{ odd}, i \neq j; \\ -\beta_{\frac{j}{2}}x_{\frac{i+1}{2}}\mu'_{\frac{i+1}{2}}\left(\bar{\mathcal{N}}\right) & , \quad i \text{ odd}, j \text{ even } j \neq i+1; \\ -\epsilon_{\frac{i}{2}}\left(\sum_{k=1}^{n} y_k\right) - y_{\frac{i}{2}}\epsilon'_{\frac{i}{2}}\left(\sum_{k=1}^{n} y_k\right) & , \quad i \text{ even}, j = i; \\ -y_{\frac{i}{2}}\epsilon'_{\frac{i}{2}}\left(\sum_{k=1}^{n} y_k\right) & , \quad i, j \text{ even}, i \neq j; \\ 0 & , \quad i \text{ even}, j \text{ odd}, \end{cases}$$

where $\bar{\mathcal{N}} = T - \sum_{k=1}^{n} \alpha_k x_k - \sum_{k=1}^{n} \beta_k y_k$ and

$$c_{ij}^k = \begin{cases} 0 & , \quad i \text{ odd}, \text{any } j; \text{ or } i \text{ even}, j \neq 2k, j \neq 2k-1; \\ b_k e^{-d_k\tau_k} y_k \left(h_k(x_k) + x_k h'_k(x_k)\right) & , \quad i = 2k, \ j = 2k-1; \\ b_k e^{-d_k\tau_k} x_k h_k(x_k) & , \quad i = 2k, \ j = 2k; \end{cases}$$

Therefore, about the stability of the boundary equilibrium points E_0 and $\tilde{E}$, we have

Theorem 2.10.

(i) *E_0 is always an unstable saddle point;*

(ii) *All $\tilde{E}$ are locally asymptotically stable if $b_k\tilde{P}_k h_k(\tilde{P}_k)e^{-d_k\tau_k} < \epsilon_k(0)$ for all $k = 1, 2, \ldots, n$ and they are unstable if $b_k\tilde{P}_k h_k(\tilde{P}_k)e^{-d_k\tau_k} > \epsilon_k(0)$ for some $k = 1, 2, \ldots, n$.*

Proof. **(i)** At the equilibrium point E_0, $J^k\big|_{E_0} = [0]$ and

$$J^0 = \left(\begin{array}{cc|cc|c|cc} \mu_1(T) & 0 & & & & & \\ 0 & -\epsilon_1(0) & & 0 & \cdots & & 0 \\ \hline & & \mu_2(T) & 0 & & & \\ & 0 & 0 & -\epsilon_2(0) & \cdots & & 0 \\ \hline \vdots & & \vdots & & \ddots & \vdots & \\ \hline & & & & & \mu_n(T) & 0 \\ 0 & & 0 & & \cdots & 0 & -\epsilon_n(0) \end{array}\right).$$

Obviously E_0 is unstable saddle point since there are positive eigenvalues $\mu_i(T)$ and negative eigenvalues $-\epsilon_i(0)$, $i = 1, 2, \ldots, n$.
(ii) Let $\xi_i = b_i e^{-d_i \tau_i}$. The characteristic equation $\Delta(\lambda) = 0$ at the point $\tilde{E}$ becomes

$$\det\begin{pmatrix} \lambda + \alpha_1 \tilde{P}_1 \mu_1'(0) & \beta_1 \tilde{P}_1 \mu_1'(0) + h_1\left(\tilde{P}_1\right) & \alpha_2 \tilde{P}_1 \mu_1'(0) & \cdots & \beta_n \tilde{P}_1 \mu_1'(0) \\ 0 & \lambda + \epsilon_1(0) - \xi_1 \tilde{P}_1 h_1\left(\tilde{P}_1\right) e^{-\lambda\tau_1} & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ \alpha_1 \tilde{P}_n \mu_n'(0) & \beta_1 \tilde{P}_n \mu_n'(0) & \alpha_2 \tilde{P}_n \mu_n'(0) & \cdots & \beta_n \tilde{P}_n \mu_n'(0) + h_n\left(\tilde{P}_n\right) \\ 0 & 0 & 0 & \cdots & \lambda + \epsilon_n(0) - \xi_n \tilde{P}_n h_n\left(\tilde{P}_n\right) e^{-\lambda\tau_n} \end{pmatrix} = 0$$

which is,

$$\Delta(\lambda) = \left(\prod_{k=1}^{n}\left(\lambda+\epsilon_k(0)-\xi_k\tilde{P}_k h_k\left(\tilde{P}_k\right)e^{-\lambda\tau_k}\right)\right) \times \begin{vmatrix} \lambda+\alpha_1\tilde{P}_1\mu_1'(0) & \alpha_2\tilde{P}_1\mu_1'(0) & \cdots & \alpha_n\tilde{P}_1\mu_1'(0) \\ \alpha_1\tilde{P}_2\mu_2'(0) & \lambda+\alpha_2\tilde{P}_2\mu_2'(0) & \cdots & \alpha_n\tilde{P}_2\mu_2'(0) \\ \vdots & \vdots & \ddots & \vdots \\ \alpha_1\tilde{P}_n\mu_n'(0) & \alpha_2\tilde{P}_n\mu_n'(0) & \cdots & \lambda+\alpha_n\tilde{P}_n\mu_n'(0) \end{vmatrix} = 0.$$

Since

$$\begin{vmatrix} \lambda+\alpha_1\tilde{P}_1\mu_1'(0) & \alpha_2\tilde{P}_1\mu_1'(0) & \cdots & \alpha_n\tilde{P}_1\mu_1'(0) \\ \alpha_1\tilde{P}_2\mu_2'(0) & \lambda+\alpha_2\tilde{P}_2\mu_2'(0) & \cdots & \alpha_n\tilde{P}_2\mu_2'(0) \\ \vdots & \vdots & \ddots & \vdots \\ \alpha_1\tilde{P}_n\mu_n'(0) & \alpha_2\tilde{P}_n\mu_n'(0) & \cdots & \lambda+\alpha_n\tilde{P}_n\mu_n'(0) \end{vmatrix} = \lambda^{n-1}\left(\lambda+\sum_{i=1}^{n}\left(\alpha_i\tilde{P}_i\mu_i'(0)\right)\right),$$

then the characteristic equation becomes

$$\Delta(\lambda) = \lambda^{n-1}\left(\prod_{k=1}^{n}\left(\lambda+\epsilon_k(0)-\xi_k\tilde{P}_k h_k\left(\tilde{P}_k\right)e^{-\lambda\tau_k}\right)\right)\left(\lambda+\sum_{i=1}^{n}\left(\alpha_i\tilde{P}_i\mu_i'(0)\right)\right) = 0.$$

From the result in Theorem (2.2), it is easy to see that if $\xi_k\tilde{P}_k h_k(\tilde{P}_k) < \epsilon_k(0)$ for all $k = 1, 2, \ldots, n$, then $\tilde{E}$ is locally asymptotically stable and unstable if $b_k\tilde{P}_k h_k(\tilde{P}_k)e^{-d_k\tau_k} > \epsilon_k(0)$ for some $k = 1, 2, \ldots, n$. □

Although we cannot show the global attractivity of each equilibrium point $\tilde{E}$, with parallel proof in Theorem (2.6), we have the following "group" property.

Theorem 2.11. *When $b_i M_i e^{-d_i\tau_i} < \epsilon_i(0)$ for all $i = 1, \ldots, n$, the solutions of (2.15) satisfy $\sum_{i=1}^{n} \alpha_i P_i(t) \longrightarrow T$ and $Z_i(t) \longrightarrow 0$ for all $i = 1, \ldots, n$ as $t \longrightarrow \infty$.*

As we know from the previous section that, even for the system with one patch ($n = 1$), the existence and the number of positive equilibrium point are uncertain which depend on the choices of the functions, parameters and time delay as well. With general functions and $n > 1$, this becomes more complicated. Biologically, it is almost impossible to know the environment for the coexistence of each species. However, we know that, if each species can coexist, at least the maturation time delay for each predator cannot be long. In fact, assume there exists a positive equilibrium point $E^* = (P_1^*, Z_1^*, P_2^*, Z_2^*, \ldots, P_n^*, Z_n^*)$, then from

$$\frac{\epsilon_i \left(\sum_{k=1}^{n} Z_k^* \right) e^{d_i\tau_i}}{b_i} = P_i^* h_i\left(P_i^*\right) \leq M_i,$$

and the hypothesis (C_3), we know that τ_i must be less than

$$\tau_{\max} = \min\left\{ \frac{1}{d_i} \ln\left(\frac{b_i M_i}{\epsilon_i(0)} \right) : i = 1, 2, \ldots, n \right\}.$$

The condition $\tau < \tau_{\max}$ is necessary for the existence of such E^* in (2.15).

With some particular choice of the functions, we maybe able to obtain some better result.

Case I: When the total predation terms from higher trophic level from higher trophic level $\epsilon_i \left(\sum_{k=1}^{n} Z_k \right)$ are constants for all $i = 1, 2, \ldots, n$, then the positive equilibrium point E^* exists and is unique under certain condition, which is an extension of Theorem (2.7).

Theorem 2.12. *When* $\epsilon_i \left(\sum_{k=1}^{n} Z_k \right) = c_i$ *are constants and* $b_i M_i e^{-d_i \tau_i} > c_i$ *for* $i = 1, 2, \ldots, n$, *there exist a unique positive equilibrium point* E^* *in (2.15).*

Case II: When the n parallel food chains are symmetric, that is, the growth functions for all taxa at the same trophic level have the same functional forms and the same parameter values, the maturation delay for each predator is the same, then the system has at least a positive equilibrium point E^* with $P_1^* = P_2^* = \ldots = P_n^* := P^*$, and $Z_1^* = Z_2^* = \ldots = Z_n^* := Z^*$ and the characteristic equation $\Delta(\lambda) = 0$ has the form,

$$
\begin{vmatrix}
\lambda+l_1+l_2\alpha & l_3+l_2\beta & l_2\alpha & l_2\beta & l_2\alpha & l_2\beta & \cdots \\
m_1e^{-\tau\lambda} & \lambda+m_2e^{-\tau\lambda}+m_3+m_4 & 0 & m_4 & 0 & m_4 & \cdots \\
l_2\alpha & l_2\beta & \lambda+l_1+l_2\alpha & l_3+l_2\beta & l_2\alpha & l_2\beta & \cdots \\
0 & m_4 & m_1e^{-\tau\lambda} & \lambda+m_2e^{-\tau\lambda}+m_3+m_4 & 0 & m_4 & \cdots \\
l_2\alpha & l_2\beta & l_2\alpha & l_2\beta & \lambda+l_1+l_2\alpha & l_3+l_2\beta & \cdots \\
0 & m_4 & 0 & m_4 & m_1e^{-\tau\lambda} & \lambda+m_2e^{-\tau\lambda}+m_3+m_4 & \cdots \\
\vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \ddots
\end{vmatrix} = 0,
$$

which is equal to

$$\Delta(\lambda) = \det\left(A_1 A_2^{n-1}\right) = 0,$$

where

$$A_1 = \begin{pmatrix} \lambda + l_1 + n\alpha l_2 & l_3 + n l_2 \beta \\ m_1 e^{-\tau\lambda} & \lambda + m_3 + n\beta m_4 + m_2 e^{-\tau\lambda} \end{pmatrix}$$

and

$$A_2 = \begin{pmatrix} \lambda + l_1 & l_3 \\ m_1 e^{-\tau\lambda} & \lambda + m_3 + m_2 e^{-\tau\lambda} \end{pmatrix},$$

with

$$\begin{aligned} l_1 &= P^* Z^* h'_*, \quad l_2 = P^* \mu'_*, \quad l_3 = P^* h_*, \\ m_1 &= -b e^{-d\tau} Z^* (h_* + P^* h'_*),\ m_2 = -b e^{-d\tau} l_3,\ m_3 = \epsilon_*,\ m_4 = Z^* \epsilon'_*. \end{aligned}$$

Comparing with the result in [Arm99], without the maturation delay, the effect from A_2 does not affect the stability of the system if the predator functional response is stabilizing. However, the introduction of the delay in the maturation time, the system becomes much more involved, we can expect the system to exhibit rich dynamics, especially when the system owns some symmetry. Certainly it is not trivial, we leave the theoretical analysis for future research, and give some numerical simulations in

the last chapter.

The main part of Chapter (2) is presented in the conference BIOMAT 2013 International Symposium on Mathematical and Computational Biology and the paper is accepted by the BIOMAT [ADY14].

Chapter 3

Dynamics on a General Stage Structured n Parallel Food Chains With Migration Between Patches

3.1 Introduction

In Chapter (2), we consider the model including n parallel food chains with maturation delay and no interaction between patches is involved. However, phytoplankton migration from deep sea to the surface is essential due to lack of nutrients or because of light, the growth of phytoplankton depend on sunlight to photosynthesise [Oll99].

And since there are plenty of phytoplankton in the surface ocean, many types of zooplankton migrate deeper into the water during the day and come up at night to avoid fish and other predators, this migration is based on factors like age, sex and the season [BC09].

Many authors assumed different migration rates for both predator and prey species. For instance, the authors constructed a two patches model with migration of both the predator and the prey in [RH11], and assumed the migration of the predator dependent on the population of the prey in each patch, while the prey migration in a constant rate, [Jan94] provided a model with two patches and assumed that the prey does not migrate and the predator in the patch with a higher density will migrate to the patch with a lower density, [AP07] assumed that predators migrate with a constant migration rates, while the prey migration depends on the predator density and [PM07] considered a predator-prey model in a two-patches environment and assumed that migration between patches is faster than prey growth and considered the prey (predator) migration rates depend on the predator (prey) density.

3.2 The Model

In this section, we assume there are interactions between patches and propose a more complex model for the multi-patch predator-prey interactions, with migration between all patches:

$$\begin{aligned} \frac{dP_i}{dt} &= P_i[\mu_i(\mathcal{N}) - Z_i h_i(P_i)] + \sum_{\substack{k=1 \\ k\neq i}}^{n}(m_k^+ P_k - m_i^- P_i), \\ \frac{dZ_i}{dt} &= b_i e^{-d_i\tau_i} P_i(t-\tau_i) Z_i(t-\tau_i) h_i(P_i(t-\tau_i)) - Z_i\epsilon_i\left(\sum_{k=1}^{n} Z_k\right) \\ &\qquad + \sum_{\substack{k=1 \\ k\neq i}}^{n}(s_k^+ Z_k - s_i^- Z_i), \end{aligned} \tag{3.1}$$

where m_k^+ and s_k^+ denote the migration rates of the prey and predator species from patch k to i and m_i^- and s_i^- denote the emigration rates of the prey and predator species from patch i to other patches, respectively. All functions $\mu_i(\mathcal{N})$, $h_i(P_i)$ and $\epsilon_i(Z)$ satisfy hypothesis (C_1 - C_3).

For simplicity, we assume that all the migration rate be the same constant m, and

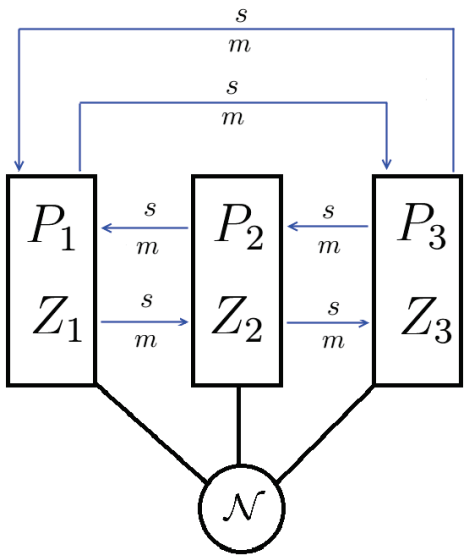


Figure 3.1: Three parallel food chains with migration between patches.

emigration rate be the constant s, then the system (3.1) becomes

$$\begin{aligned}
\frac{dP_i}{dt} &= P_i[\mu_i(\mathcal{N}) - Z_i h_i(P_i)] + m\left(\sum_{\substack{k=1\\k\neq i}}^{n} P_k - (n-1)\,P_i\right), \\
\frac{dZ_i}{dt} &= b_i e^{-d_i\tau_i} P_i(t-\tau_i) Z_i(t-\tau_i) h_i(P_i(t-\tau_i)) - Z_i\epsilon_i\left(\sum_{k=1}^{n} Z_k\right) \\
&\qquad + s\left(\sum_{\substack{k=1\\k\neq i}}^{n} Z_k - (n-1)\,Z_i\right).
\end{aligned} \tag{3.2}$$

When $n = 3$, the connection among three patches is shown in Fig. (3.1). To understand the general dynamical properties produced in Eq. (3.2), we start from

the simplest case.

3.3 2 Parallel Phytoplankton Zooplankton Patches With Migration of Both Species

We start with the case when $n = 2$ which is rewritten as

$$\begin{aligned}
\frac{dP_1}{dt} &= P_1[\mu_1(\mathcal{N}) - Z_1 h_1(P_1)] + m\,(P_2 - P_1)\,, \\
\frac{dZ_1}{dt} &= b_1 e^{-d_1\tau_1} P_1(t-\tau_1) Z_1(t-\tau_1) h_1(P_1(t-\tau_1)) - Z_1\epsilon_1\,(Z_1 + Z_2) + s\,(Z_2 - Z_1)\,, \\
\frac{dP_2}{dt} &= P_2[\mu_2(\mathcal{N}) - Z_2 h_2(P_2)] + m\,(P_1 - P_2)\,, \qquad (3.3) \\
\frac{dZ_2}{dt} &= b_2 e^{-d_2\tau_2} P_2(t-\tau_2) Z_2(t-\tau_2) h_2(P_2(t-\tau_2)) - Z_2\epsilon_2\,(Z_1 + Z_2) + s\,(Z_1 - Z_2)\,.
\end{aligned}$$

With $\mathcal{N} = T - \alpha_1 P_1 - \alpha_2 P_2 - \beta_1 Z_1 - \beta_2 Z_2$.

The purpose of this section is to analyze and demonstrate the population dynamics of various species in model (3.3) by finding the ultimate upper bound for the interacting populations and exploring the local stability of all the possible equilibrium solutions.

Theorem 3.1. *Given the initial condition $P_i(0), Z_i(0) \in C^+$, $i = 1, 2$, then under the hypothesis (C_1 - C_3), the solutions of (3.3) are nonnegative in $X = C^2 \times C^2$. In*

addition, if $\epsilon_1(0), \epsilon_2(0) > 0$ *then all the solutions are ultimately bounded in* X*.*

Proof. $P_i(t) \geq 0$ and $Z_i(t) \geq 0$, $i = 1, 2$ for all $t > 0$ through an initial value in C^+; this follows from [Smi95] (Theorem 5.2.1 on page 81).

Further, from

$$P_1' + P_2' = (P_1 + P_2)' = P_1 \left[\mu_1 (\mathcal{N}) - Z_1 h_1 (P_1)\right] + P_2 \left[\mu_2 (\mathcal{N}) - Z_2 h_2 (P_2)\right] \tag{3.4}$$

Under the hypothesis (C_1), $\mu_i(\mathcal{N})$ is increasing function with respect to $\mathcal{N}$, then

$$\begin{aligned} (P_1 + P_2)' &\leq P_1 \mu_1 (\mathcal{N}) + P_2 \mu_2 (\mathcal{N}) \\ &\leq P_1 \mu_1 (T - \alpha_1 P_1 - \alpha_2 P_2) + P_2 \mu_2 (T - \alpha_1 P_1 - \alpha_2 P_2) \\ &\leq (P_1 + P_2)\, \hat{\mu} (T - \alpha_1 P_1 - \alpha_2 P_2) \end{aligned}$$

Where $\hat{\mu}(\cdots) = \mu_1(\cdots) + \mu_2(\cdots)$. Since $\hat{\mu}(T - \alpha_1 P_1 - \alpha_2 P_2)$ is decreasing with respect to $\alpha_1 P_1 + \alpha_2 P_2$, we have

$$(P_1 + P_2)' \leq (P_1 + P_2)\, \hat{\mu} (T - \tilde{\alpha} (P_1 + P_2)).$$

Where $\tilde{\alpha} = \min\{\alpha_1, \alpha_2\}$. Since $\hat{\mu}(0) = 0$, we know $\lim\limits_{t \to \infty} \sup (P_1 + P_2) \leq T/\tilde{\alpha}$, implying $P_1(t) + P_1(t)$ is ultimately bounded.

Let $P(t) = P_1(t) + P_2(t)$, $Z(t) = Z_1(t) + Z_2(t)$ and

$$S(t) = \tilde{b}^2 e^{-2\hat{d}\hat{\tau}}(P(t-\tau_1) + P(t-\tau_2)) + \tilde{b}e^{-\hat{d}\hat{\tau}} Z(t).$$

With $\tilde{b} = \max\{b_1, b_2\}$, $\hat{d} = \min\{d_1, d_2\}$ and $\hat{\tau} = \min\{\tau_1, \tau_2\}$, we can obtain

$$\begin{aligned}
S'(t) &= \tilde{b}^2 e^{-2\hat{d}\hat{\tau}} P_1(t-\tau_1)\mu_1(\mathcal{N}_1) - \tilde{b}^2 e^{-2\hat{d}\hat{\tau}} Z_1(t-\tau_1)P_1(t-\tau_1)h_1(P_1(t-\tau_1)) \\
&\quad + \tilde{b}^2 e^{-2\hat{d}\hat{\tau}} P_2(t-\tau_1)\mu_2(\mathcal{N}_1) - \tilde{b}^2 e^{-2\hat{d}\hat{\tau}} Z_2(t-\tau_1)P_2(t-\tau_1)h_2(P_2(t-\tau_1)) \\
&\quad + \tilde{b}^2 e^{-2\hat{d}\hat{\tau}} P_1(t-\tau_2)\mu_1(\mathcal{N}_2) - \tilde{b}^2 e^{-2\hat{d}\hat{\tau}} Z_1(t-\tau_2)P_1(t-\tau_2)h_1(P_1(t-\tau_2)) \\
&\quad + \tilde{b}^2 e^{-2\hat{d}\hat{\tau}} P_2(t-\tau_2)\mu_2(\mathcal{N}_2) - \tilde{b}^2 e^{-2\hat{d}\hat{\tau}} Z_2(t-\tau_2)P_2(t-\tau_2)h_2(P_2(t-\tau_2)) \\
&\quad + \tilde{b}b_1 e^{-\hat{d}\hat{\tau}-d_1\tau_1} Z_1(t-\tau_1)P_1(t-\tau_1)h_1(P_1(t-\tau_1)) - \tilde{b}e^{-\hat{d}\hat{\tau}} Z_1(t)\epsilon_1 \left(Z_1(t) + Z_2(t)\right) \\
&\quad + \tilde{b}b_2 e^{-\hat{d}\hat{\tau}-d_2\tau_2} Z_2(t-\tau_2)P_2(t-\tau_2)h_2(P_2(t-\tau_2)) - \tilde{b}e^{-\hat{d}\hat{\tau}} Z_2(t)\epsilon_2 \left(Z_1(t) + Z_2(t)\right),
\end{aligned}$$

where $\mathcal{N}_i = T - \alpha_1 P_1(t-\tau_i) - \alpha_2 P_2(t-\tau_i) - \beta_1 Z_1(t-\tau_i) - \beta_2 Z_2(t-\tau_i)$, $i = 1, 2$.

From the hypothesis (C_3), $\epsilon_i(Z) \geq 0$ for all $Z \geq 0$, we obtain

$$
\begin{aligned}
S'(t) &\leq \tilde{b}^2 e^{-2\hat{d}\hat{\tau}} P_1(t-\tau_1)\mu_1(\mathcal{N}_1) - \tilde{b}^2 e^{-2\hat{d}\hat{\tau}} Z_1(t-\tau_1)P_1(t-\tau_1)h_1(P_1(t-\tau_1)) \\
&\quad + \tilde{b}^2 e^{-2\hat{d}\hat{\tau}} P_2(t-\tau_1)\mu_2(\mathcal{N}_1) + \tilde{b}^2 e^{-2\hat{d}\hat{\tau}} P_1(t-\tau_2)\mu_1(\mathcal{N}_2) \\
&\quad + \tilde{b}^2 e^{-2\hat{d}\hat{\tau}} P_2(t-\tau_2)\mu_2(\mathcal{N}_2) - \tilde{b}^2 e^{-2\hat{d}\hat{\tau}} Z_2(t-\tau_2)P_2(t-\tau_2)h_2(P_2(t-\tau_2)) \\
&\quad + \tilde{b}^2 e^{-2\hat{d}\hat{\tau}} Z_1(t-\tau_1)P_1(t-\tau_1)h_1(P_1(t-\tau_1)) - \tilde{b} e^{-\hat{d}\hat{\tau}} Z_1(t)\epsilon_1\left(Z_1(t)+Z_2(t)\right) \\
&\quad + \tilde{b}^2 e^{-2\hat{d}\hat{\tau}} Z_2(t-\tau_2)P_2(t-\tau_2)h_2(P_2(t-\tau_2)) - \tilde{b} e^{-\hat{d}\hat{\tau}} Z_2(t)\epsilon_2\left(Z_1(t)+Z_2(t)\right) \\
&= \tilde{b}^2 e^{-2\hat{d}\hat{\tau}} P_1(t-\tau_1)\mu_1(\mathcal{N}_1) + \tilde{b}^2 e^{-2\hat{d}\hat{\tau}} P_2(t-\tau_1)\mu_2(\mathcal{N}_1) \\
&\quad + \tilde{b}^2 e^{-2\hat{d}\hat{\tau}} P_1(t-\tau_2)\mu_1(\mathcal{N}_2) + \tilde{b}^2 e^{-2\hat{d}\hat{\tau}} P_2(t-\tau_2)\mu_2(\mathcal{N}_2) \\
&\quad - \tilde{b} e^{-\hat{d}\hat{\tau}} Z_1(t)\epsilon_1\left(Z_1(t)+Z_2(t)\right) - \tilde{b} e^{-\hat{d}\hat{\tau}} Z_2(t)\epsilon_2\left(Z_1(t)+Z_2(t)\right) \\
&\leq \tilde{b}^2 e^{-2\hat{d}\hat{\tau}} \mu_1(T)P_1(t-\tau_1) + \tilde{b}^2 e^{-2\hat{d}\hat{\tau}} \mu_2(T)P_2(t-\tau_1) \\
&\quad + \tilde{b}^2 e^{-2\hat{d}\hat{\tau}} \mu_1(T)P_1(t-\tau_2) + \tilde{b}^2 e^{-2\hat{d}\hat{\tau}} \mu_2(T)P_2(t-\tau_2) \\
&\quad - \tilde{b} e^{-\hat{d}\hat{\tau}} Z_1(t)\epsilon_1(0) - \tilde{b} e^{-\hat{d}\hat{\tau}} Z_2(t)\epsilon_2(0) \\
&\leq \tilde{\mu}(T)\tilde{b}^2 e^{-2\hat{d}\hat{\tau}}(P(t-\tau_1)+P(t-\tau_2)) - \hat{\epsilon}(0)\tilde{b} e^{-\hat{d}\hat{\tau}} Z(t) \\
&= \tilde{b}^2 e^{-2\hat{d}\hat{\tau}} \tilde{\mu}(T)(P(t-\tau_1)+P(t-\tau_2)) + \tilde{b}^2 e^{-2\hat{d}\hat{\tau}} \hat{\epsilon}(0)\left(P(t-\tau_1)+P(t-\tau_2)\right) \\
&\quad - \hat{\epsilon}(0)\left(\tilde{b}^2 e^{-2\hat{d}\hat{\tau}}(P(t-\tau_1)+P(t-\tau_2)) + \tilde{b} e^{-\hat{d}\hat{\tau}} Z(t)\right) \\
&\leq \frac{2T\tilde{b}^2 e^{-2\hat{d}\hat{\tau}}}{\tilde{\alpha}}\left(\tilde{\mu}(T)+\hat{\epsilon}(0)\right) - \hat{\epsilon}(0)\, S(t),
\end{aligned}
$$

with $\tilde{\mu}(T) = \max\{\mu_1(T), \mu_2(T)\}$ and $\hat{\epsilon}(0) = \min\{\epsilon_1(0), \epsilon_2(0)\}$. If $\hat{\epsilon}(0) > 0$ then $\limsup_{t\to\infty} S(t) \leq \frac{2T\tilde{b}^2 e^{-2\hat{d}\hat{\tau}}}{\tilde{\alpha}\hat{\epsilon}(0)} (\tilde{\mu}(T) + \hat{\epsilon}(0))$. Therefore, $P_1(t)$, $P_2(t)$, $Z_1(t)$ and $Z_2(t)$ are ultimately bounded in X. □

Remark 3.1.

- *Since the right hand side of $P_i', Z_i', i = 1, 2$ are related to mP_j, sZ_j, $i \neq j$, in (3.3), respectively, we need [Smi95] (Theorem 5.2.1 on page 81) to prove the positivity. While in Theorem (2.9), the positivity is proved by standard arguments for P_i and comparison theory for Z_i.*

- *Without migrations, in Theorem (2.9), we have upper bound for each patch individually*

$$P_i(t) \leq \frac{T}{\alpha_i} \quad \text{and} \quad b_i e^{-d_i\tau_i} P_i(t) + Z_i(t) \leq \frac{b_i T e^{-d_i\tau_i}(\mu_i(T) + \epsilon_i(0)}{\alpha_i \epsilon_i(0)},$$

  $i = 1, 2$. With migrations, we can provide upper bound for a linear combination of all solutions in Theorem (3.1).

- **Existence and Stability of Boundary Equilibrium Points**

We can see that system (3.3) has a trivial equilibrium point $E_0 = (0, 0, 0, 0)$. Moreover, the stability of E_0 is given in the following result.

Theorem 3.2. *E_0 is always an unstable saddle point.*

Proof. The linearization of (3.3) at E_0 is

$$\begin{aligned} x_1'(t) &= (\mu_1(T) - m)x_1(t) + mx_2(t), \\ y_1'(t) &= -(\epsilon_1(0) + s)y_1(t) + sy_2(t), \\ x_2'(t) &= mx_1(t) + (\mu_2(T) - m)x_2(t), \\ y_2'(t) &= sy_1(t) - (\epsilon_2(0) + s)y_2(t). \end{aligned} \tag{3.5}$$

The characteristic equation of (3.5) is

$$\begin{aligned} \Delta(\lambda) &= \left[\lambda^2 + (2m - \mu_1(T) - \mu_2(T))\lambda + \mu_1(T)\mu_2(T) - m\left(\mu_1(T) + \mu_2(T)\right)\right] \\ &\quad \times \left[\lambda^2 + (\epsilon_1(0) + \epsilon_2(0) + 2s)\lambda + \epsilon_1(0)\epsilon_2(0) + s\epsilon_2(0) + s\epsilon_1(0)\right]. \end{aligned}$$

Let $h(\lambda) = \lambda^2 + (2m - \mu_1(T) - \mu_2(T))\lambda + \mu_1(T)\mu_2(T) - m\left(\mu_1(T) + \mu_2(T)\right)$. $h(\lambda) = 0$ has real roots since the discriminant of $h(\lambda)$, $4m^2 + \left(\mu_1(T) - \mu_2(T)\right)^2 > 0$ always holds. Assume $h(\lambda) = 0$ has two negative real roots then

$$2m - \mu_1(T) - \mu_2(T) > 0 \quad \text{and} \quad \mu_1(T)\mu_2(T) - m\left(\mu_1(T) + \mu_2(T)\right) > 0.$$

Which is equivalent to

$$m > \frac{\mu_1(T) + \mu_2(T)}{2} \quad \text{and} \quad \frac{\mu_1(T)\mu_2(T)}{\mu_1(T) + \mu_2(T)} > m.$$

Thus $\frac{2\mu_1(T)\mu_2(T)}{(\mu_1(T)+\mu_2(T))^2} > 1$ which leads to a contradiction. Therefore $h(\lambda) = 0$ has at least one positive real root, implying E_0 is unstable saddle point. □

Next, we discuss the existence of a predator-free equilibrium point under the hypotheses $(C_1 - C_3)$.

Proposition 3.1. *Givin the hypothesis $(C_1 - C_3)$, then a unique predator-free equilibrium point $\tilde{E} = (\mathcal{T}, 0, \mathcal{T}, 0)$ exists for system (3.3) with $\mathcal{T} := \frac{T}{\alpha_1+\alpha_2}$.*

Proof. A predator-free equilibrium point for two patches must satisfy

$$\begin{aligned} P_1\mu_1\left(T - \alpha_1 P_1 - \alpha_2 P_2\right) + mP_2 - mP_1 &= 0, \\ P_2\mu_2\left(T - \alpha_1 P_1 - \alpha_2 P_2\right) + mP_1 - mP_2 &= 0. \end{aligned} \tag{3.6}$$

It is easy to check that $\tilde{E}$ satisfies (3.6).

To prove the uniqueness of such $\tilde{E}$, it's easy to see that when one of $P_i, (i = 1, 2)$ is zero, another one must be zero as well, which excludes the case with one prey species can survive and another cannot.

Further, adding two equations in (3.6) yields

$$\tilde{P}_1\mu_1\left(T-\alpha_1\tilde{P}_1-\alpha_2\tilde{P}_2\right)+\tilde{P}_2\mu_2\left(T-\alpha_1\tilde{P}_1-\alpha_2\tilde{P}_2\right)=0.$$

When $P_i>0$, due to $\mu_i\geq 0,(i=1,2)$, we have $\alpha_1P_1+\alpha_2P_2=T$. Substituting into (3.6), we obtain $P_1=P_2=\frac{T}{\alpha_1+\alpha_2}$. □

Remark 3.2. *(i) If either $Z_1=0$ or $Z_2=0$ then system (3.3) has a unique predator-free equilibrium point $\tilde{E}=(\mathcal{T},0,\mathcal{T},0)$.*

(ii) The result in Proposition(3.1) implies the effect of migrations. With migrations between both patches, only one positive predator-free equilibrium point exists for system (3.3). But without migration, $s=0$ and $m=0$, in Remark (2.1) we can see that system (3.3) has infinite number of predator-free equilibrium points with the form $\tilde{E}=(\tilde{\alpha}_1\tilde{P}_1,0,\tilde{\alpha}_2\tilde{P}_2,0)$ such that $\tilde{\alpha}_1\tilde{P}_1+\tilde{\alpha}_2\tilde{P}_2=T$.

After we have obtained the existence of the predator-free equilibrium point $\tilde{E}$, we discuss its stability. At first, for the special case with $\tau_1=\tau_2:=\tau$, by denoting minimum and maximum of the corresponding parameters by $\hat{\cdot}$, $\tilde{\cdot}$, respectively, we know $\tilde{E}$ is globally attractive under certain condition, which is given in the following theorem.

Theorem 3.3. *Assume $\tau_1 = \tau_2 := \tau > 0$. When $\tilde{b}\tilde{M}e^{-\hat{d}\tau} < \hat{\epsilon}(0)$ then the solutions of (3.3) satisfy $P_i \to \mathcal{T}$ and $Z_i \to 0$, $i = 1, 2$.*

Proof. Adding the second and the forth equations in (3.3), we have

$$\begin{aligned} Z_1' + Z_2' &= b_1 e^{-d_1\tau} P_1(t-\tau) h_1(P_1(t-\tau)) Z_1(t-\tau) - \epsilon_1(Z_1 + Z_2) \\ &\quad + b_2 e^{-d_2\tau} P_2(t-\tau) h_2(P_2(t-\tau)) Z_2(t-\tau) - \epsilon_2(Z_1 + Z_2). \end{aligned}$$

Let $\delta > 0$. Following the hypotheses (C_1) and (C_3), we have $\epsilon_i(Z_1 + Z_2) \geq \hat{\epsilon}(0)$ and $P_i(t-\tau)h_i(P_i(t-\tau)) \leq \tilde{M}$ for any $t > t_\delta + \tau$. Thus

$$Z_1' + Z_2' \leq \tilde{b}\tilde{M}e^{-\hat{d}\tau}(Z_1(t-\tau) + Z_2(t-\tau)) - \hat{\epsilon}(0)(Z_1(t) + Z_2(t)).$$

The comparison theory implies that $Z_1(t) + Z_2(t)$ is bounded above by the solution of

$$u'(t) = \tilde{b}\tilde{M}e^{-\hat{d}\tau}u(t-\tau) - \hat{\epsilon}(0)u(t), \quad t > t_\delta + \tau$$

such that $u(t) = Z_1(t) + Z_2(t)$ for $t \in [t_\delta, t_\delta + \tau]$. Since $\tilde{b}\tilde{M}e^{-\hat{d}\tau} < \hat{\epsilon}(0)$, Lemma (2.1) implies that $\lim_{t\to\infty}(Z_1(t) + Z_2(t)) = 0$. Since both $Z_1(t)$ and $Z_2(t)$ are nonnegative from Theorem (3.1), we have $\lim_{t\to\infty} Z_i(t) = 0$, $i = 1, 2$.

By the existences and uniqueness of the predator-free equilibrium point $\tilde{E}$ in

Proposition (3.1) and Remark (3.2), we obtain $\lim_{t\to\infty} P_i(t) = \mathcal{T}$, $i = 1, 2$. □

While in general, beyond the strong condition $\tilde{b}\tilde{M}e^{-\hat{d}\tau} < \hat{\epsilon}(0)$ and/or with two different delays τ_1, τ_2, we can discuss the local stability of $\tilde{E}$ by setting $x_1 = P_1 - \mathcal{T}$, $y_1 = Z_1$,$x_2 = P_2 - \mathcal{T}$ and $y_2 = Z_2$. Then the linearization of (3.3) at $\tilde{E}$ is

$$\begin{aligned}
x_1'(t) &= a_{11}x_1(t) + a_{12}y_1(t) + a_{13}x_2(t) + a_{14}y_2(t),\\
y_1'(t) &= a_{22}y_1(t) + a_{24}y_2(t) + b_{22}y_1(t-\tau_1),\\
x_2'(t) &= a_{31}x_1(t) + a_{32}y_1(t) + a_{33}x_2(t) + a_{34}y_2(t),\\
y_2'(t) &= a_{42}y_1(t) + a_{44}y_2(t) + c_{44}y_2(t-\tau_2),
\end{aligned} \tag{3.7}$$

where

$$\begin{aligned}
a_{11} &= -\alpha_1\mathcal{T}\mu_1{}'(0) - m < 0, \quad a_{12} = -\beta_1\mathcal{T}\mu_1{}'(0) - \mathcal{T}h_1(\mathcal{T}) < 0,\\
a_{13} &= -\alpha_2\mathcal{T}\mu_1{}'(0) + m, \quad a_{14} = -\beta_2\mathcal{T}\mu_1{}'(0) < 0,\\
a_{22} &= -\epsilon_1(0) - s < 0, \quad a_{24} = s > 0, \quad b_{22} = b_1e^{-\tau_1 d_1}\mathcal{T}h_1(\mathcal{T}) > 0,\\
a_{31} &= -\alpha_1\mathcal{T}\mu_2{}'(0) + m, \quad a_{32} = -\beta_1\mathcal{T}\mu_2{}'(0) < 0,\\
a_{33} &= -\alpha_2\mathcal{T}\mu_2{}'(0) - m < 0, \quad a_{34} = -\beta_2\mathcal{T}\mu_2{}'(0) - \mathcal{T}h_2(\mathcal{T}) < 0,\\
a_{42} &= s > 0, \quad a_{44} = -\epsilon_2(0) - s < 0, \quad c_{44} = b_2e^{-\tau_2 d_2}\mathcal{T}h_2(\mathcal{T}) > 0.
\end{aligned}$$

The characteristic equation of (3.7) is

$$\Delta(\lambda, \tau_1, \tau_2) = G(\lambda)K(\lambda, \tau_1, \tau_2) = 0, \tag{3.8}$$

with

$$\begin{aligned} G(\lambda) &= \lambda^2 - (a_{11} + a_{33})\lambda + a_{11}a_{33} - a_{13}a_{31}, \\ K(\lambda, \tau_1, \tau_2) &= \left(\lambda - a_{22} - b_{22}e^{-\lambda\tau_1}\right)\left(\lambda - a_{44} - c_{44}e^{-\lambda\tau_2}\right) - a_{24}a_{42}. \end{aligned}$$

It is easy to check that $G(\lambda) = 0$ has two roots negative real part, since both $-(a_{11} + a_{33}), a_{11}a_{33} - a_{13}a_{31} = mT(\alpha_1 + \alpha_2)(\mu_1' + \mu_2') > 0$.

Now, $K(\lambda, \tau_1, \tau_2)$ can be written as

$$K(\lambda, \tau_1, \tau_2) = \lambda^2 + k_1\lambda + k_2 + e^{-\lambda\tau_1}(k_3\lambda + k_4) + e^{-\lambda\tau_2}(k_5\lambda + k_6) + k_7e^{-\lambda(\tau_1+\tau_2)}, \tag{3.9}$$

where

$$\begin{aligned} k_1 &= -(a_{22} + a_{44}) > 0, \quad k_2 = a_{22}a_{44} - a_{24}a_{42} > 0, \quad k_3 = -b_{22} < 0, \\ k_4 &= b_{22}a_{44} < 0, \quad k_5 = -c_{44} < 0, \quad k_6 = c_{44}a_{22} < 0, \quad k_7 = b_{22}c_{44} > 0. \end{aligned} \tag{3.10}$$

When $\tau_1 = \tau_2 = 0$,

$$K(\lambda, 0, 0) = \lambda^2 + (k_1 + k_3 + k_5)\,\lambda + (k_2 + k_4 + k_6 + k_7) = 0.$$

Following the Routh-Hurwitz stability criterion we have

Proposition 3.2. *At $\tau_1 = \tau_2 = 0$, the predator-free equilibrium point $\tilde{E}$ is locally asymptotically stable if and only if*

$$k_1 + k_3 + k_5 > 0 \quad \& \quad k_2 + k_7 + k_4 + k_6 > 0. \tag{$\tilde{\mathbf{H}}_0$}$$

First, we consider a simple case $\tau_1 = \tau_2 := \tau > 0$, Eq. (3.9) becomes

$$K(\lambda, \tau) = \lambda^2 + k_1\lambda + k_2 + (k_3 + k_5)\,\lambda e^{-\lambda\tau} + (k_4 + k_6)\,e^{-\lambda\tau} + k_7 e^{-2\lambda\tau} \tag{3.11}$$

The eigenvalue $\lambda = 0$ is not a root of $K(\lambda, \tau) = 0$, since

$$\begin{aligned} K(0, \tau) &= k_2 + k_4 + k_6 + k_7 \\ &= (\epsilon_1(0) + b_1 e^{-\tau_1 d_1}\mathcal{T}h_1(\mathcal{T}))(\epsilon_2(0) + b_2 e^{-\tau_2 d_2}\mathcal{T}h_2(\mathcal{T})) \\ &+ s(\epsilon_1(0) + \epsilon_2(0) + b_1 e^{-\tau_1 d_1}\mathcal{T}h_1(\mathcal{T}) + b_2 e^{-\tau_2 d_2}\mathcal{T}h_2(\mathcal{T})) > 0. \end{aligned}$$

For a pure imaginary root of (3.11), let $\lambda = i\omega$, $\omega > 0$, then separate the real and imaginary parts to obtain

$$\begin{aligned} \omega^2 - k_2 &= (k_3 + k_5)\,\omega \sin \omega\tau + (k_4 + k_6)\cos \omega\tau + k_7 \cos 2\omega\tau \\ k_1\omega &= -(k_3 + k_5)\,\omega \cos \omega\tau + (k_4 + k_6)\sin \omega\tau + k_7 \sin 2\omega\tau. \end{aligned} \tag{3.12}$$

Squaring and adding both equations of (3.12) lead to

$$\begin{aligned} &\omega^4 - \left[2k_2 + (k_3 + k_5)^2 - k_1^2\right]\omega^2 + \left[k_2^2 - (k_4 + k_6)^2 - k_7^2\right] \\ &= 2\,(k_4 + k_6)\,k_7 \cos \omega\tau - 2\omega\,(k_3 + k_5)\,k_7 \sin \omega\tau. \end{aligned}$$

Since $k_7 > 0, (k_4 + k_6), (k_3 + k_5) < 0, \omega > 0$, then

$$\omega^4 - \left[2k_2 + (k_3 + k_5)^2 - k_1^2\right]\omega^2 + \left[k_2^2 - (k_4 + k_6)^2 - k_7^2\right] \leq -2\,(k_4 + k_6)\,k_7 - 2\tau\,(k_3 + k_5)\,k_7\omega^2,$$

which is equivalent to

$$\omega^4 - \left[2k_2 + (k_3 + k_5)^2 - k_1^2 - 2\tau\,(k_3 + k_5)\,k_7\right]\omega^2 + \left[k_2^2 - (k_4 + k_6 - k_7)^2\right] \leq 0.$$

From the latter inequality we see that if

$$2k_2 + (k_3 + k_5)^2 - k_1^2 - 2\tau (k_3 + k_5) k_7 < 0 \tag{3.13}$$

and

$$k_2^2 - (k_4 + k_6 - k_7)^2 > 0, \tag{3.14}$$

then there is no such $\omega > 0$, that is, (3.11) will has no roots with zero real part.

Theorem 3.4. *Assume* $\tau_1 = \tau_2 := \tau > 0$ *and*

$$A = \frac{b_1 \mathcal{T} h_1(\mathcal{T}) (\epsilon_2(0) + s) + b_2 \mathcal{T} h_2(\mathcal{T}) (\epsilon_1(0) + s) + b_1 b_2 \mathcal{T}^2 h_1(\mathcal{T}) h_2(\mathcal{T})}{\epsilon_1(0) + \epsilon_2(0) + s(\epsilon_1(0) + \epsilon_2(0))}.$$

Let

$$\bar{\tau} = \frac{(\epsilon_1(0) + \epsilon_2(0) + s)^2 - 2(b_1 \mathcal{T} h_1(\mathcal{T}) + b_2 \mathcal{T} h_2(\mathcal{T}))^2}{4 b_2 b_2 \mathcal{T}^2 (b_1 \mathcal{T} h_1(\mathcal{T}) + b_2 \mathcal{T} h_2(\mathcal{T})) h_1(\mathcal{T}) h_2(\mathcal{T})} > 0,$$

$$\bar{\bar{\tau}} = \begin{cases} \frac{1}{\hat{d}} \ln A, \ A > 1; \\ 0, \ 0 < A < 1, \end{cases}$$

and $\bar{\tau} > \bar{\bar{\tau}}$, *where* $\hat{d} = \min\{d_1, d_2\}$. *If the predator-free equilibrium point* $\tilde{E}$ *is locally asymptotically stable at* $\tau^* \in (\bar{\bar{\tau}}, \bar{\tau})$ *then* $\tilde{E}$ *is locally asymptotically stable for all*

$\tau \in (\bar{\bar{\tau}}, \bar{\tau})$.

Proof. Firstly, we consider the left side of (3.13). Substituting the expression $k_1, \ldots, k_7$ from (3.10), we have

$$\begin{aligned}
& 2\left(\epsilon_1(0)\epsilon_2(0) + s(\epsilon_1(0) + \epsilon_2(0))\right) + \left(b_1\mathcal{T}h_1(\mathcal{T})e^{-d_1\tau} + b_2\mathcal{T}h_2(\mathcal{T})e^{-d_2\tau}\right)^2 \\
& -(\epsilon_1(0) + \epsilon_2(0) + 2s)^2 \\
& +2\tau\left(b_1\mathcal{T}h_1(\mathcal{T})e^{-d_1\tau} + b_2\mathcal{T}h_2(\mathcal{T})e^{-d_2\tau}\right) b_1b_2\mathcal{T}^2h_1(\mathcal{T})h_2(\mathcal{T})e^{-(d_2+d_1)\tau} \\
< \; & 2\left(\epsilon_1(0)\epsilon_2(0) + s(\epsilon_1(0) + \epsilon_2(0))\right) + \left(b_1\mathcal{T}h_1(\mathcal{T}) + b_2\mathcal{T}h_2(\mathcal{T})\right)^2 \\
& -(\epsilon_1(0) + \epsilon_2(0) + 2s)^2 + 2\tau\left(b_1\mathcal{T}h_1(\mathcal{T}) + b_2\mathcal{T}h_2(\mathcal{T})\right) b_1b_2\mathcal{T}^2h_1(\mathcal{T})h_2(\mathcal{T}) \\
< \; & \left(b_1\mathcal{T}h_1(\mathcal{T}) + b_2\mathcal{T}h_2(\mathcal{T})\right)^2 + 2\tau\left(b_1\mathcal{T}h_1(\mathcal{T}) + b_2\mathcal{T}h_2(\mathcal{T})\right) b_1b_2\mathcal{T}^2h_1(\mathcal{T})h_2(\mathcal{T}) \\
& -\left(\epsilon_1(0)^2 + \epsilon_2(0)^2 + 4s^2\right) \\
< \; & \left(b_1\mathcal{T}h_1(\mathcal{T}) + b_2\mathcal{T}h_2(\mathcal{T})\right)^2 + 2\tau\left(b_1\mathcal{T}h_1(\mathcal{T}) + b_2\mathcal{T}h_2(\mathcal{T})\right) b_1b_2\mathcal{T}^2h_1(\mathcal{T})h_2(\mathcal{T}) \\
& -\frac{1}{2}(\epsilon_1(0) + \epsilon_2(0) + 2s)^2.
\end{aligned}$$

So if

$$\tau < \bar{\tau} := \frac{\left(\epsilon_1(0) + \epsilon_2(0) + s\right)^2 - 2\left(b_1\mathcal{T}h_1(\mathcal{T}) + b_2\mathcal{T}h_2(\mathcal{T})\right)^2}{4b_2b_2\mathcal{T}^2\left(b_1\mathcal{T}h_1(\mathcal{T}) + b_2\mathcal{T}h_2(\mathcal{T})\right)h_1(\mathcal{T})h_2(\mathcal{T})}$$

then (3.13) holds.

Secondly, since $k_2 - k_4 - k_6 + k_7$ is always positive, we can see (3.14) is true if and

only if $k_2 + k_4 + k_6 - k_7 > 0$. From

$$\begin{aligned} & k_2 + k_4 + k_6 - k_7 \\ = \; & \epsilon_1(0)\epsilon_2(0) + s\epsilon_1(0) + s\epsilon_2(0) - (\epsilon_2(0) + s)\, b_1 \mathcal{T} h_1(\mathcal{T}) e^{-d_1\tau} \\ & - (\epsilon_1(0) + s)\, b_2 \mathcal{T} h_2(\mathcal{T}) e^{-d_2\tau} - b_1 b_2 \mathcal{T}^2 h_1(\mathcal{T}) h_2(\mathcal{T}) e^{-(d_2+d_1)\tau} \\ > \; & \epsilon_1(0)\epsilon_2(0) + s\epsilon_1(0) + s\epsilon_2(0) \qquad (3.15) \\ & - \left((\epsilon_2(0) + s)\, b_1 \mathcal{T} h_1(\mathcal{T}) + (\epsilon_1(0) + s)\, b_2 \mathcal{T} h_2(\mathcal{T}) + b_1 b_2 \mathcal{T}^2 h_1(\mathcal{T}) h_2(\mathcal{T})\right) e^{-\hat{d}\tau}, \end{aligned}$$

where $\hat{d} = \min\{d_1, d_2\}$. So if $A > 1$, then (3.15) holds for $\tau > \bar{\bar{\tau}} := \frac{1}{\hat{d}} \ln A$ and when $0 < A < 1$, (3.15) holds for all $\tau > 0$. Therefore, when $\tau \in (\bar{\bar{\tau}}, \bar{\tau})$, both (3.13) and (3.14) hold. Thus, (3.11) has no pure imaginary roots.

At τ^*, $\tilde{E}$ is locally asymptotically stable. Since there are no sign changes in roots of $K(\lambda, \tau) = 0$ for $\tau \in (\bar{\bar{\tau}}, \bar{\tau})$, $\tilde{E}$ is locally asymptotically stable on this interval. □

With two different delays in Eq.(3.9), we start with $\tau_1 = 0$ and $\tau_2 = \tau_2^* > 0$, where τ_2^* satisfy that $K(\lambda, 0, \tau_2^*)$ have roots with negative real parts under certain conditions (which can be found using similar argument as we discussed previously), then by using *Rouchs Theorem* regarding τ_1 as a parameter in Eq.(3.9) and following [[KC82], [WR99]] there exists $\tau_1^* = \tau_1(\tau_2^*) > 0$ such that $\tilde{E}$ is stable for $\tau_1 \in (0, \tau_1^*)$. Beyond this interval, it's possible to have bifurcations similar in Chapter (2). We

give a munerical Example (6) in Chapter (4).

We can see that $K(\lambda, \tau_1, \tau_2)$ is independent of the prey migration rate m, that is, m does not affect the stability of the predator-free equilibrium point $\tilde{E}$. On the other hand, when the predator migration rate $s = 0$, $\tilde{E}$ is locally asymptotically stable if $b_k \mathcal{T} h_k(\mathcal{T}) e^{-d_k \tau_k} < \epsilon_k(0)(\ k = 1, 2)$ in Theorem (2.10); but when $s > 0$, the stability at $\tilde{E}$ depends on the functions $h_k(P_k)$, $\epsilon_k(Z)$ and the values of $\mathcal{T},\ b_k,\ d_k, \tau_k$ and becomes complicated since the coefficients K_i $(i = 1, \ldots, 7)$ all are related to s. However, with particular choices, it is possible to find stability conditions involving the value of s [KT94]. Since our model is more general and with delay, the analysis becomes more complicated. We leave this as our future work.

- **Existence and Stability of Positive Equilibrium**

When system (3.3) exists a positive equilibrium point, the values of $P_i^*, Z_i^*, i = 1, 2$ must satisfy

$$\begin{aligned}
P_1^*[\mu_1(\mathcal{N}^*) - Z_1^* h_1(P_1^*)] - m\,(P_2^* - P_1^*) &= 0,\\
b_1 e^{-d_1\tau_1} P_1^* Z_1^* h_1(P_1^*) - Z_1^*\epsilon_1\,(Z_1^* + Z_2^*) - s\,(Z_2^* - Z_1^*) &= 0,\\
P_2^*[\mu_2(\mathcal{N}^*) - Z_2^* h_2(P_2^*)] - m\,(P_1^* - P_2^*) &= 0,\\
b_2 e^{-d_2\tau_2} P_2^* Z_2^* h_2(P_2^*) - Z_2^*\epsilon_2\,(Z_1^* + Z_2^*) - s\,(Z_1^* - Z_2^*) &= 0,
\end{aligned} \tag{3.16}$$

with $\mathcal{N}^* = T - \alpha_1 P_1^* - \alpha_2 P_2^* - \beta_1 Z_1^* - \beta_2 Z_2^*$. From the second and forth equations of (3.16), we have

$$\begin{aligned}
\frac{Z_1^*\epsilon_1\,(Z_1^* + Z_2^*) + s\,(Z_2^* - Z_1^*)}{Z_1^*} &= b_1 e^{-d_1\tau_1} P_1^* h_1(P_1^*) \le b_1 e^{-d_1\tau_1} M_1,\\
\frac{Z_2^*\epsilon_2\,(Z_1^* + Z_2^*) + s\,(Z_1^* - Z_2^*)}{Z_2^*} &= b_2 e^{-d_2\tau_2} P_2^* h_2(P_2^*) \le b_2 e^{-d_2\tau_2} M_2,
\end{aligned} \tag{3.17}$$

respectively. Since $\epsilon_i(0) \le \epsilon_i(Z_1^* + Z_2^*)$ for $i = 1, 2$, we have

$$\begin{aligned}
\frac{Z_2^*}{Z_1^*} &\le \frac{b_1 e^{-d_1\tau_1} M_1 + s - \epsilon_1(0)}{s}\\
\frac{Z_1^*}{Z_2^*} &\le \frac{b_2 e^{-d_2\tau_2} M_2 + s - \epsilon_2(0)}{s}.
\end{aligned}$$

provided $b_i e^{-d_i\tau_i} M_i + s > \epsilon_i(0),\ i = 1, 2$. Thus

$$\frac{s}{b_1 e^{-d_1\tau_1} M_1 + s - \epsilon_1(0)} \leq \frac{b_2 e^{-d_2\tau_2} M_2 + s - \epsilon_2(0)}{s},$$

which leads to

$$s \leq \frac{(b_1 e^{-d_1\tau_1} M_1 - \epsilon_1(0))(b_2 e^{-d_2\tau_2} M_2 - \epsilon_2(0))}{(\epsilon_1(0) - b_1 e^{-d_1\tau_1} M_1) + (\epsilon_2(0) - b_2 e^{-d_2\tau_2} M_2)}. \tag{$\mathbf{H}_*$}$$

Therefore,

Lemma 3.1. *Let $\tau_1 = \tau_2 := \tau$. When*

$$(b_1 M_1 - \epsilon_1(0))\,(b_2 M_2 - \epsilon_2(0)) + s(b_1 M_1 + b_1 M_1 - \epsilon_1(0) - \epsilon_2(0)) < 0,$$

E^* does not exist for any feasible $\tau > 0$.

The condition ($\mathbf{H}_*$) is necessary for the existence of a positive equilibrium point $E^* = (P_1^*, Z_1^*, P_2^*, Z_2^*)$ in (3.3), but is not a sufficient condition in general.

To discuss the existence of E^*, define $H_i(P_i) = P_i h_i(P_i)$ for $i = 1, 2$, With the

hypothesis (C_2), $H_i(P_i)$ is positive and increasing on $(0, \frac{T}{\alpha_1+\alpha_2})$, we can obtain

$$\begin{aligned} P_1^* &= H_1^{-1}\left(\frac{Z_1^*\epsilon_1\left(Z_1^*+Z_2^*\right)+s\left(Z_1^*-Z_2^*\right)}{b_1 e^{-d_1\tau_1}Z_1^*}\right); \\ P_2^* &= H_2^{-1}\left(\frac{Z_2^*\epsilon_2\left(Z_1^*+Z_2^*\right)+s\left(Z_2^*-Z_1^*\right)}{b_2 e^{-d_2\tau_2}Z_2^*}\right), \end{aligned} \tag{3.18}$$

from the second and forth equations of (3.16), respectively. While Z_1^* and Z_2^* are the positive solutions of the following equations:

$$\begin{aligned} &H_1^{-1}\left(\frac{Z_1^*\epsilon_1\left(Z_1^*+Z_2^*\right)+s\left(Z_1^*-Z_2^*\right)}{b_1 e^{-d_1\tau_1}Z_1^*}\right)\mu_1\left(\mathcal{N}^*\right)-\frac{Z_1^*\epsilon_1\left(Z_1^*+Z_2^*\right)+s\left(Z_1^*-Z_2^*\right)}{b_1 e^{-d_1\tau_1}} \\ &+m\left(H_2^{-1}\left(\frac{Z_2^*\epsilon_2\left(Z_1^*+Z_2^*\right)+s\left(Z_2^*-Z_1^*\right)}{b_2 e^{-d_2\tau_2}Z_2^*}\right)-H_1^{-1}\left(\frac{Z_1^*\epsilon_1\left(Z_1^*+Z_2^*\right)+s\left(Z_1^*-Z_2^*\right)}{b_1 e^{-d_1\tau_1}Z_1^*}\right)\right)=0; \end{aligned} \tag{3.19}$$

$$\begin{aligned} &H_2^{-1}\left(\frac{Z_2^*\epsilon_2\left(Z_1^*+Z_2^*\right)+s\left(Z_2^*-Z_1^*\right)}{b_2 e^{-d_2\tau_2}Z_2^*}\right)\mu_2\left(\mathcal{N}^*\right)-\frac{Z_2^*\epsilon_2\left(Z_1^*+Z_2^*\right)+s\left(Z_2^*-Z_1^*\right)}{b_2 e^{-d_2\tau_2}} \\ &+m\left(H_1^{-1}\left(\frac{Z_1^*\epsilon_1\left(Z_1^*+Z_2^*\right)+s\left(Z_1^*-Z_2^*\right)}{b_1 e^{-d_1\tau_1}Z_1^*}\right)-H_2^{-1}\left(\frac{Z_2^*\epsilon_2\left(Z_1^*+Z_2^*\right)+s\left(Z_2^*-Z_1^*\right)}{b_2 e^{-d_2\tau_2}Z_2^*}\right)\right)=0, \end{aligned} \tag{3.20}$$

with

$$\mathcal{N}^*=T-\alpha_1 H_1^{-1}\left(\frac{Z_1^*\epsilon_1\left(Z_1^*+Z_2^*\right)+s\left(Z_1^*-Z_2^*\right)}{b_1 e^{-d_1\tau_1}Z_1^*}\right)-\alpha_2 H_2^{-1}\left(\frac{Z_2^*\epsilon_2\left(Z_1^*+Z_2^*\right)+s\left(Z_2^*-Z_1^*\right)}{b_2 e^{-d_2\tau_2}Z_2^*}\right)-\beta_1 Z_1^*-\beta_2 Z_2^*,$$

which is impossible to find an analytical solution in general.

With fixed parameters, feasible values of delays and certain functions, for instance, choose the functions [RH11] given in Table (3.1), we have $E^*=(0.093, 0.57, 0.048, .56)$ when $\tau_1=0.4$ and $\tau_2=0.7$.

	$h(P)$	$\mu(N)$	$\epsilon(Z)$
Patch 1	$\frac{1}{P+1}$	$\frac{N}{T}$	0.02
Patch 2	$\frac{2}{P+2}$	$\frac{N}{T}$	0.03

Table 3.1: Existence of E_1^* with $\alpha_i = \beta_i = 1$, $b_i = 0.25$, $d_i = 0.01$, $s = 0.1$, $m = 0.6$ and $T = 7$ for $i = 1, 2$.

When the two parallel food chains are symmetric (the growth functions for all taxa at the same trophic level have the same functional forms and the same parameter values, the maturation delay for each predator is the same), system (3.3) becomes

$$\begin{aligned} \frac{dP_i}{dt} &= P_i\left[\mu\left(\mathcal{N}\right) - Z_i h\left(P_i\right)\right] + m\left(P_j - P_i\right), \\ \frac{dZ_i}{dt} &= be^{-d\tau} P_i\left(t-\tau\right) Z_i\left(t-\tau\right) h\left(P_i\left(t-\tau\right)\right) - Z_i\epsilon\left(Z_i + Z_j\right) + s\left(Z_j - Z_i\right), \end{aligned} \tag{3.21}$$

$i, j \in \{1, 2\},\ i \neq j$ and $\mathcal{N} = T - \alpha(P_1 + P_2) - \beta(Z_1 + Z_2)$. And ($\mathbf{H}_*$) becomes

$$0 \leq (be^{-d\tau}M + 2s - \epsilon(0))(be^{-d\tau}M - \epsilon(0)). \tag{$\mathbf{H}_*'$}$$

Proposition 3.3. *(i) Assume $h(P)$ is an increasing function on the interval $[0, \frac{T}{2\alpha}]$.*

If the positive equilibrium point E^* exists, then it must have the form of (P^*, Z^*, P^*, Z^*).

(ii) When $h(P)$ is not increasing on the interval $[0, \frac{T}{2\alpha}]$, beside the positive equilib-

rium point (P^*, Z^*, P^*, Z^*)*, it is possible to have other positive equilibrium point with different* P_i^* *and* Z_i^**,* $i = 1, 2$.

Proof. (i) Assume $(P_1^*, Z_1^*, P_2^*, Z_2^*)$ is a positive equilibrium point. Then, we can prove $P_1^* = P_2^*$ and $Z_1^* = Z_2^*$. Otherwise, from the first and third equations in (3.21), we have

$$m(P_1^{*^2} - P_2^{*^2}) = Z_2^* P_1^* H(P_2^*) - Z_1^* P_2^* H(P_1^*). \tag{3.22}$$

Similarly, from the second and forth equations in (3.21), we have

$$s(Z_2^{*^2} - Z_1^{*^2}) = be^{-d\tau} Z_1^* Z_2^* (H(P_2^*) - H(P_1^*)). \tag{3.23}$$

Suppose $P_1^* > P_2^*$, then by (3.23) and the hypothesis (C_2), we obtain $Z_1^* > Z_2^*$.

For the right hand side of (3.22), we have

$$\begin{aligned} Z_2^* P_1^* H(P_2^*) - Z_1^* P_2^* H(P_1^*) &< Z_1^* P_1^* H(P_2^*) - Z_1^* P_2^* H(P_1^*) \\ &= Z_1^* P_1^* P_2^* (h(P_2^*) - h(P_1^*)) < 0 \end{aligned}$$

when $h(p)$ is increasing, which leads to a contradiction, because the left hand side of (3.22) is positive.

While similarly, if $P_1^* < P_2^*$, then $Z_1^* < Z_2^*$ and the left hand side of (3.22) is

negative while the right hand side is positive.

(ii) If the positive equilibrium exists, obviously, (P^*, Z^*, P^*, Z^*) satisfies (3.18), (3.19) and (3.20). Without additional condition, we cannot exclude any other form in E^*. □

When the positive equilibrium point $E^* = (P^*, Z^*, P^*, Z^*)$ exists, the linearization of (3.21) at E^*, by sitting $x_1 = P_1 - P^*$, $y_1 = Z_1 - Z^*$, $x_2 = P_2 - P^*$ and $y_2 = Z_2 - Z^*$, is

$$\begin{aligned}
\frac{dx_1}{dt} &= a_{11}x_1(t) + a_{12}y_1(t) + a_{13}x_2(t) + a_{14}y_2(t),\\
\frac{dy_1}{dt} &= a_{22}y_1(t) + a_{24}y_2(t) + b_{21}x_1(t-\tau) + b_{22}y_1(t-\tau),\\
\frac{dx_2}{dt} &= a_{13}x_1(t) + a_{14}y_1(t) + a_{11}x_2(t) + a_{12}y_2(t),\\
\frac{dy_2}{dt} &= a_{24}y_1(t) + a_{22}y_2(t) + b_{21}x_2(t-\tau) + b_{22}y_2(t-\tau),
\end{aligned} \tag{3.24}$$

with

$$\begin{aligned}
a_{11} &= \mu^* - Z^*h^* - \alpha P^*\mu'_* - P^*Z^*h'_* - m,\ a_{12} = -\beta P^*\mu'_* - P^*h^* < 0,\\
a_{13} &= -\alpha P^*\mu'_* + m,\ a_{14} = -\beta P^*\mu'_* < 0,\ a_{22} = -Z^*\epsilon'_* - \epsilon^* - s < 0\\
a_{24} &= -Z^*\epsilon'_* + s,\ b_{21} = be^{-d\tau}Z^*\left(P^*h'_* + h^*\right) > 0,\ b_{22} = be^{-d\tau}P^*h^* > 0,
\end{aligned}$$

where μ^*, h^*, ϵ^* denotes the value of the function μ, h, ϵ and $\mu'_*, h'_*, \epsilon'_*$ denotes the value of the derivative of the associated function at (P^*, Z^*, P^*, Z^*) respectively.

Remark 3.3 ([Sil00], [AM05]-page 117)**.** *When the block matrices are square matrices of the same order, then the determinant of a matrix of the form* $\left(\begin{array}{c|c} A & B \\ \hline B & A \end{array}\right)$ *is* $\det(A-B)\det(A+B)$.

In our case, $A = \begin{pmatrix} \lambda - a_{11} & -a_{12} \\ -b_{21}e^{-d\tau} & \lambda - a_{22} - b_{22}e^{-d\tau} \end{pmatrix}$ and $B = \begin{pmatrix} -a_{13} & -a_{14} \\ 0 & -a_{24} \end{pmatrix}$.
Thus the characteristic equation of (3.24) is

$$\Delta(\lambda, \tau) = \Phi(\lambda, \tau)\Psi(\lambda, \tau) = 0, \tag{3.25}$$

where

$$\Phi(\lambda, \tau) = \lambda^2 + \phi_1\lambda + \phi_2 + \phi_3 e^{-\lambda\tau} + \zeta\lambda e^{-\lambda\tau}, \tag{3.26}$$

$$\Psi(\lambda, \tau) = \lambda^2 + \psi_1\lambda + \psi_2 + \psi_3 e^{-\lambda\tau} + \zeta\lambda e^{-\lambda\tau}, \tag{3.27}$$

$$\begin{aligned} \phi_1 &= a_{24} + a_{13} - a_{22} - a_{11},\ \phi_2 = (a_{24} - a_{22})(a_{13} - a_{11}), \\ \phi_3 &= b_{21}(a_{14} - a_{12}) - b_{22}(a_{13} - a_{11}),\ \psi_1 = -(a_{24} + a_{13} + a_{22} + a_{11}), \\ \psi_2 &= (a_{24} + a_{22})(a_{13} + a_{11}),\ \psi_3 = b_{21}(a_{14} + a_{12}) + b_{22}(a_{13} - a_{11}),\ \zeta = -b_{22} < 0. \end{aligned}$$

As we discussed previously in Chapter (2), we can find parallel conditions for stability. Since there conditions are not related to the original system, we omit the "abstract" conditions here, we will give numerical results Example (7) in Chapter (5).

3.4 n Parallel Phytoplankton Zooplankton Patches with Migration

As we know from the previous section that, for the system (3.2) with two patches, the local stability analysis of the equilibrium points are very harsh even when all patches are symmetric. With $n > 2$, this becomes more complicated. In this section, we only present some properties of the general model (3.2) with n parallel phytoplankton-

zooplankton patches with migration. Rewrite the system (3.2) as

$$\begin{aligned}
\frac{dP_1}{dt} &= P_1[\mu_1(\mathcal{N}) - Z_1 h_1(P_1)] + m\left(\sum_{k=2}^{n} P_k - (n-1)\,P_1\right), \\
\frac{dZ_1}{dt} &= b_1 e^{-d_1\tau_1} P_1(t-\tau_1) Z_1(t-\tau_1) h_1(P_1(t-\tau_1)) - Z_1\epsilon_i\left(\sum_{k=1}^{n} Z_k\right) \\
&\qquad + s\left(\sum_{k=2}^{n} Z_k - (n-1)\,Z_1\right), \\
&\vdots \\
\frac{dP_n}{dt} &= P_n[\mu_i(\mathcal{N}) - Z_n h_n(P_n)] + m\left(\sum_{k=1}^{n-1} P_k - (n-1)\,P_n\right), \\
\frac{dZ_n}{dt} &= b_n e^{-d_n\tau_n} P_n(t-\tau_n) Z_n(t-\tau_n) h_n(P_n(t-\tau_n)) - Z_n\epsilon_i\left(\sum_{k=n}^{n} Z_k\right) \\
&\qquad + s\left(\sum_{k=1}^{n-1} Z_k - (n-1)\,Z_n\right).
\end{aligned} \tag{3.28}$$

Similarly, we have the following results:

Theorem 3.5. *Given the hypothesis (C_1 - C_3)*

(i) If the initial condition $P_i(0), Z_i(0) \in C^+$, $i = 1, \ldots, 2$, then the solutions of (3.28) are nonnegative in $X = C^n \times C^n$. In addition, if $\epsilon_i(0) > 0$ then all the solutions are ultimately bounded in X.

(ii) In addition to the trivial equilibrium point $E_0 = \underbrace{(0, 0, \ldots, 0, 0)}_{2n}$, there is a unique

predator-free equilibrium point

$$\tilde{E} = \underbrace{\left(\frac{T}{\sum_{\alpha=1}^{n} \alpha_i}, 0, \ldots, \frac{T}{\sum_{\alpha=1}^{n} \alpha_i}, 0 \right)}_{2n}$$

When all patches are similar, it is possible to have the unique co-existed positive equilibrium point $E^* = \underbrace{(P^*, Z^*, \ldots, P^*, Z^*)}_{2n}$ under the hypothesis $(C_1 - C_3)$ and certain conditions.

To study the stability of each equilibrium point (x_1,y_1,x_2,y_2, ... ,x_n,y_n), we need to know the general form of the characteristic equation, which is,

$$\Delta(\lambda) = \det\left(\lambda I - J^0 - \sum_{k=1}^{n} J^k e^{-\lambda \tau_k} \right) = 0$$

where $J^0 = (a_{ij})$ and $J^k = \left(c_{ij}^k\right)$ are $2n \times 2n$ matrices with

$$a_{ij} = \begin{cases} -x_{\frac{i+1}{2}}\left[\alpha_{\frac{i+1}{2}}\mu'_{\frac{i+1}{2}}\left(\bar{\mathcal{N}}\right) + y_{\frac{i+1}{2}}h'_{\frac{i+1}{2}}\left(x_{\frac{i+1}{2}}\right)\right] & \\ +\left[\mu_{\frac{i+1}{2}}\left(\bar{\mathcal{N}}\right) - y_{\frac{i+1}{2}}h_{\frac{i+1}{2}}\left(x_{\frac{i+1}{2}}\right)\right] - (n-1)m & , \quad i \text{ odd}, j = i; \\ -x_{\frac{i+1}{2}}\left[\beta_{\frac{i+1}{2}}\mu'_{\frac{i+1}{2}}\left(\bar{\mathcal{N}}\right) + h_{\frac{i+1}{2}}\left(x_{\frac{i+1}{2}}\right)\right] & , \quad i \text{ odd}, \ j = i+1; \\ -\alpha_{\frac{j+1}{2}}x_{\frac{i+1}{2}}\mu'_{\frac{i+1}{2}}\left(\bar{\mathcal{N}}\right) + m & , \quad i, j \text{ odd}, i \neq j; \\ -\beta_{\frac{j}{2}}x_{\frac{i+1}{2}}\mu'_{\frac{i+1}{2}}\left(\bar{\mathcal{N}}\right) & , \quad i \text{ odd}, j \text{ even } j \neq i+1; \\ -\epsilon_{\frac{i}{2}}\left(\sum_{k=1}^{n} y_k\right) - y_{\frac{i}{2}}\epsilon'_{\frac{i}{2}}\left(\sum_{k=1}^{n} y_k\right) + (n-1)s & , \quad i \text{ even}, j = i; \\ -y_{\frac{i}{2}}\epsilon'_{\frac{i}{2}}\left(\sum_{k=1}^{n} y_k\right) + s & , \quad i, j \text{ even}, i \neq j; \\ 0 & , \quad i \text{ even}, j \text{ odd}, \end{cases}$$

where $\bar{\mathcal{N}} = T - \sum_{k=1}^{n} \alpha_k x_k - \sum_{k=1}^{n} \beta_k y_k$ and

$$c_{ij}^k = \begin{cases} 0 & , \quad i \text{ odd}, \text{any } j; \text{ or } i \text{ even}, j \neq 2k, j \neq 2k-1; \\ b_k e^{-d_k \tau_k} y_k \left(h_k(x_k) + x_k h'_k(x_k)\right) & , \quad i = 2k, \ j = 2k-1; \\ b_k e^{-d_k \tau_k} x_k h_k(x_k) & , \quad i = 2k, \ j = 2k; \end{cases}$$

With general functions, different parameters and time delay it is not trivial to analyze the local stability of equilibrium points. However, it might be easier with a particular choice of functions with more hypotheses. We will show a numerical simulation in Chapter (4).

Chapter 4

Numerical Simulations

In this chapter, we choose some different functions, parameters and time delay from literature in several examples to compliment the theoretical results given previously.

For the model (2.2), we provide examples 1-4. One patch in Ex.(1) and (2), three symmetric patches in Ex.(3) and three different patches in Ex.(4).

Example 1. $n = 1$. We take the functions and the parameters [RH11, KR08] in system (2.3) as,

$$\begin{aligned} \mu(\mathcal{N}) &= \frac{\mathcal{N}}{15+\mathcal{N}},\ h(P) = \frac{7}{P+1},\ \epsilon(Z) = 0.05 + 0.8Z \\ d &= 0.13,\ b = 0.05,\ T = 7,\ \alpha = 0.9,\ \beta = 0.4. \end{aligned} \tag{4.1}$$

First, we can calculate $\tau_{\max} = 14.968$. At $\tau = 0$, the positive equilibrium is $E_1 = (0.393, 0.061)$. By checking the condition ($\mathbf{H_0}$), we know E_1 is unstable. With delay $\tau > 0$ and the choice in (4.1), we can obtain $\tilde{\tau} \approx 9.248$ defined in (2.8), implying the existence of the positive equilibrium point when $\tau \in (0, \tilde{\tau})$. Here $\tilde{\tau} < \tau_{\max}$ gives an evidence for that $\tau < \tau_{\max}$ is necessary, but not sufficient for the existence of positive steady state. In Fig. (4.1), we plot the graphs of the functions $S_0(\tau), S_1(\tau), S_2(\tau)$ and $S_3(\tau)$ defined in (2.14) for $\tau \in (0, \tau_{\max})$. The curve of $S_1(\tau) = 0$ has one root $\tau^* = 4.347$ and is decreasing from positive to negative, indicating the positive equilibrium is unstable for $\tau \in (0, \tau^*)$ and becomes stable at τ^* before it disappears at $\tilde{\tau}$. Fig. (4.2) shows the phase portrait of the solutions with different values of τ. With small delay τ, there exists a stable limit cycle. As τ is increasing, the limit cycle is broken, the system approaches to a stable steady state, until τ is sufficient large. Biologically, when the maturation process is short, the concentration of phytoplankton and zooplankton are oscillated regularly; when this process is a little long, all the species move to a certain level with constant concentration; but if the maturation time is too long, the zooplankton cannot survive without enough prey-phytoplankton. Therefore, the maturation time control the dynamical behavior of the system.

From this example we can see that, although we have proved the uniqueness of the positive equilibrium point when $\epsilon(Z)$ is constant, the result may hold for other

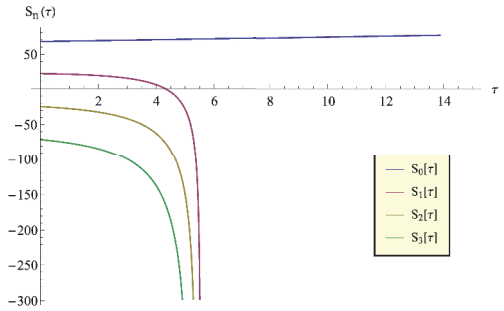


Figure 4.1: Functions $S_0(\tau), S_1(\tau), S_2(\tau)$ and $S_3(\tau)$ for $\tau \in (0, 14.968)$ corresponding to the choice in (4.1).

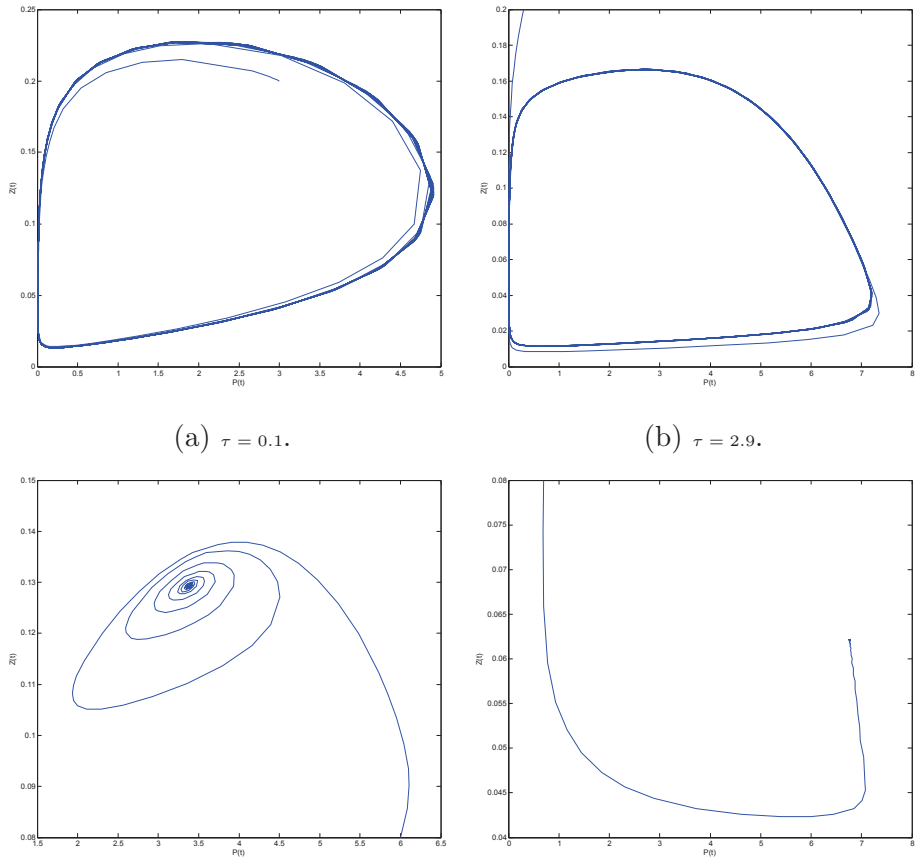
functions such as linear function.

Example 2. $n = 1$. Let

$$\mu(\mathcal{N}) = \frac{\mathcal{N}}{15+\mathcal{N}}, \ h(P) = \frac{P}{P^2+0.1}, \ \epsilon(Z) = 0.05 + 0.31Z$$
$$\alpha = \beta = 1, \ d = 0.01, \ b = 0.25, \ T = 9 \tag{4.2}$$

in system (2.3), then $\tau_{\max} = 160.944$.

With Hollong-type III functional responses, there are three positive equilibrium points $E_1 = (P_1^*, Z_1^*)$, $E_2 = (P_2^*, Z_2^*)$ and $E_3 = (P_3^*, Z_3^*)$ with $P_1^* < P_2^* < P_3^*$ for $\tau \in (0, \hat{\tau})$ with $\hat{\tau} = 38.836$, two (P_1^*, Z_1^*), (P_2^*, Z_2^*) at $\tau = \hat{\tau}$ and one (P^*, Z^*) for $\tau \in (\hat{\tau}, \tilde{\tau})$, where $\tilde{\tau} = 160.819$, see Fig. (4.3). In Fig. (4.3), the curves $f_1(P^*)$ and $f_2(P^*)$ are obtained from (2.6) since ϵ is linear. When τ is small, E_1 is stable and E_3 is unstable which can be seen in Figs. (4.4a) and (4.4b), while E_2 is a saddle point.



(a) $\tau = 0.1$.

(b) $\tau = 2.9$.

(c) $\tau = 4.5$.

(d) $\tau = 8.6$.

Figure 4.2: Phase portrait of (2.3) with different values of time delay τ and the functions and parameters given in (4.1).

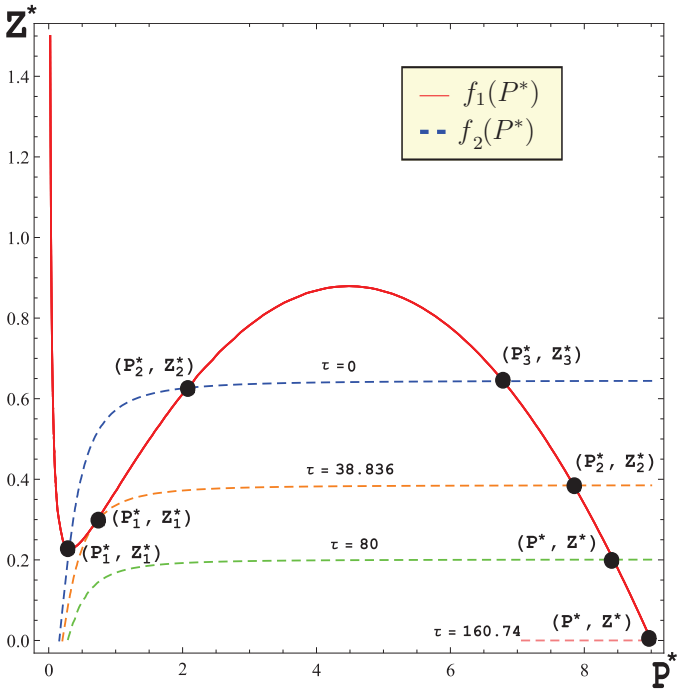
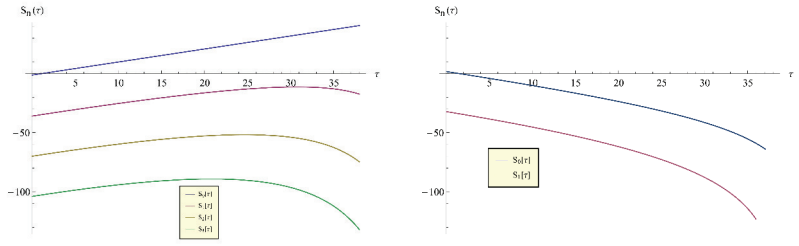


Figure 4.3: Existence of different number of positive equilibrium points with different τ.



(a) at P_1^*. (b) at P_3^*.

Figure 4.4: Graphs of the functions $S_0(\tau)$ and $S_1(\tau)$ for $\tau \in (0, \hat{\tau})$ with the functions and parameters chosen in (4.2).

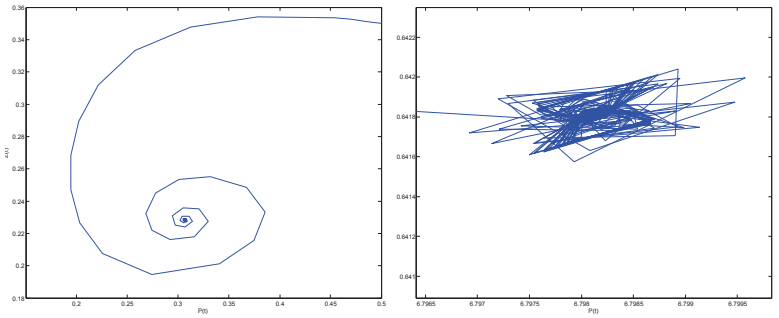
With the increasing of τ, E_1 loses the stability at $\tau^* = 1.826$ and a stable limit cycle is bifurcated, E_3 gains the stability at τ^*.

From Fig. (4.5), we can see that the stability properties of E_1 and E_3 are "local". Since E_2 is a saddle point, there exists a "basin boundary" which divides the phase plane into two parts with different dynamics in each part.

Example 3. When $n = 3$ in the system (2.2). If we choose all the functional responses and the parameters in each species are the same as, implying the patches are symmetrical,

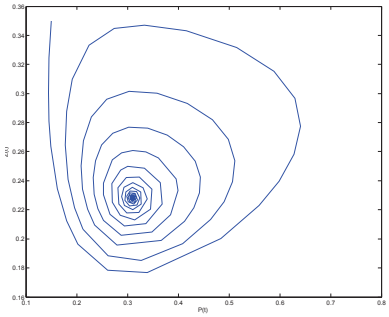
$$\begin{aligned}
&\mu_1(\mathcal{N}) = \mu_2(\mathcal{N}) = \mu_3(\mathcal{N}) = \frac{\mathcal{N}}{10+\mathcal{N}},\ h_1(P) = h_2(P) = h_3(P) = \frac{P}{P^2+1},\\
&\epsilon_1(Z) = \epsilon_2(Z) = \epsilon_3(Z) = 0.15,\ d_1 = d_2 = d_3 = 0.01,\ b_1 = b_2 = b_3 = 0.25,\\
&T = 7,\ \alpha_1 = \alpha_2 = \alpha_3 = 0.8,\ \beta_1 = \beta_2 = \beta_3 = 0.5. \qquad (4.3)
\end{aligned}$$

then $\tau_{\max} = 51.083$ and $\tilde{\tau} = 28.122$. We can check that the condition given in Theorem (2.12) is satisfied for small value of delay $\tau_1 = \tau_2 = \tau_3 := \tau$, thus there exists a unique positive equilibrium point. Since all the functional responses are the same, it is expected that all the species will be synchronized, i.e., with different initial condition, after a transaction period, each phytoplankton and each zooplankton approach to the same level by group which is confirmed in Fig. (4.6a,4.6b). With the

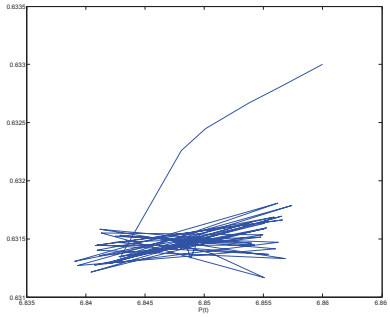


(a) $\tau = 0.2$, P_1^*.

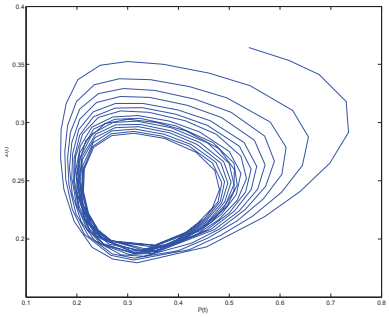
(b) $\tau = 0.2$, P_3^*.



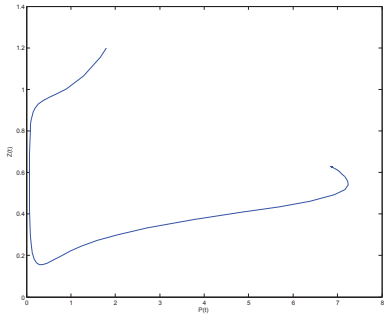
(c) $\tau = 1.5$, P_1^*.



(d) $\tau = 1.5$, P_3^*.

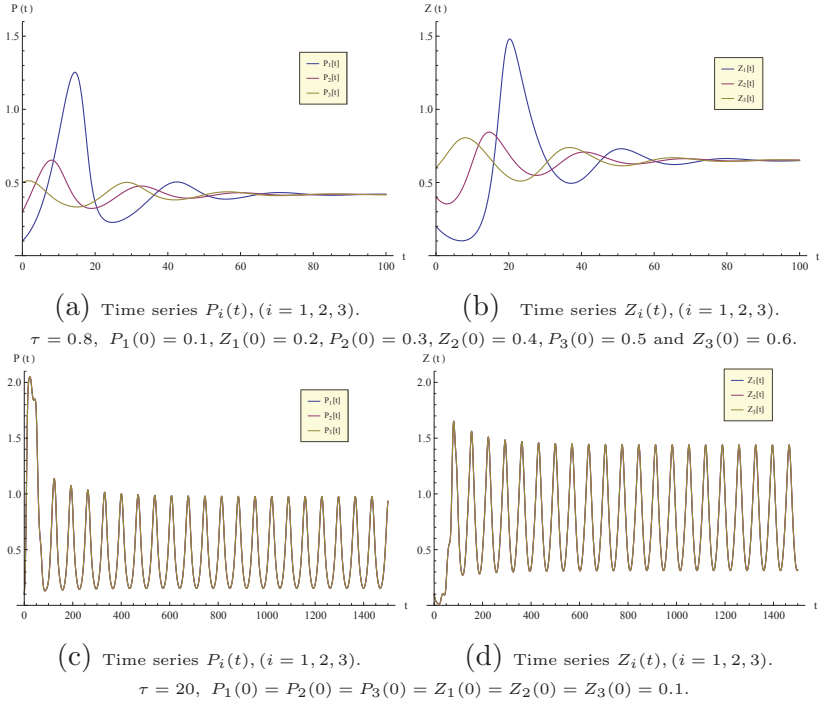


(e) $\tau = 2.1$, P_1^*.



(f) $\tau = 2.1$, P_3^*.

Figure 4.5: Phase portrait of the system (2.3) with functions and parameters given in (4.2).



(a) Time series $P_i(t), (i = 1, 2, 3)$. (b) Time series $Z_i(t), (i = 1, 2, 3)$.
$\tau = 0.8,\ P_1(0) = 0.1, Z_1(0) = 0.2, P_2(0) = 0.3, Z_2(0) = 0.4, P_3(0) = 0.5$ and $Z_3(0) = 0.6$.

(c) Time series $P_i(t), (i = 1, 2, 3)$. (d) Time series $Z_i(t), (i = 1, 2, 3)$.
$\tau = 20,\ P_1(0) = P_2(0) = P_3(0) = Z_1(0) = Z_2(0) = Z_3(0) = 0.1$.

Figure 4.6: Time series $P_i(t)$ and $Z_i(t)(i = 1, 2, 3)$ of system (2.2) with functions and parameters given in (4.3).

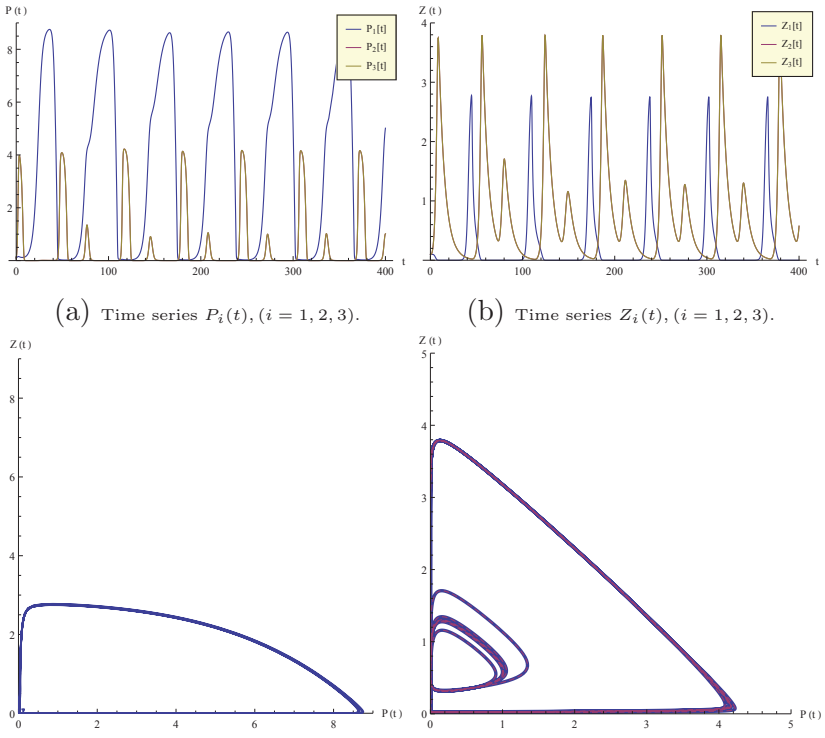
increasing of the maturation time, the steady state loses the stability and the system becomes oscillatory. See Fig. (4.6c,4.6d).

Example 4. When $n = 3$ in the system (2.2). Based on the choice in (4.3), we

take different functional responses and some parameters, such as,

$$\mu_1(\mathcal{N}) = \frac{\mathcal{N}}{15+\mathcal{N}}, \mu_2(\mathcal{N}) = \mu_3(\mathcal{N}) = \frac{4\mathcal{N}}{10+\mathcal{N}},\ h_1(P) = \frac{P}{P^2+0.1},$$
$$h_2(P) = h_3(P) = \frac{1}{P+1},\ \epsilon_1(Z) = 0.05 + 0.31Z,\ \epsilon_2(Z) = \epsilon_3(Z) = 0.15,$$
$$T = 9, d_1 = d_2 = d_3 = 0.01,\ b_1 = b_2 = b_3 = 0.25,$$
$$\alpha_1 = \alpha_2 = \alpha_3 = 1,\ \beta_1 = \beta_2 = \beta_3 = 1. \tag{4.4}$$

We can observe interesting dynamical behavior, see Fig. (4.7). With the same initial condition, when the maturation time is very small, a doubly periodic solution exists, implying a parallel condition given in ($\mathbf{H_5}$) may be satisfied for the feasible value of τ and the choice in (4.4). While when we just change the initial condition a little bit, say, keeping all are the same as that in Fig. (4.7) except changing $Z_2(0)$ from 0.1 to 0.2, then the doubly periodic orbit is disappeared, although a periodic solution still exists and the second and the third patches have almost the same behavior, see Fig. (4.8). Therefore the dynamical behavior is sensitive to the initial condition. Is it possible to have chaotic motion and/or does this due to the partial symmetry of the system since we choose two of the three patches have same response? We leave these as our future pursuit. As the maturation time is relative large, even with the same initial condition, the double periods coincide, see Fig. (4.9).



(a) Time series $P_i(t), (i = 1, 2, 3)$.

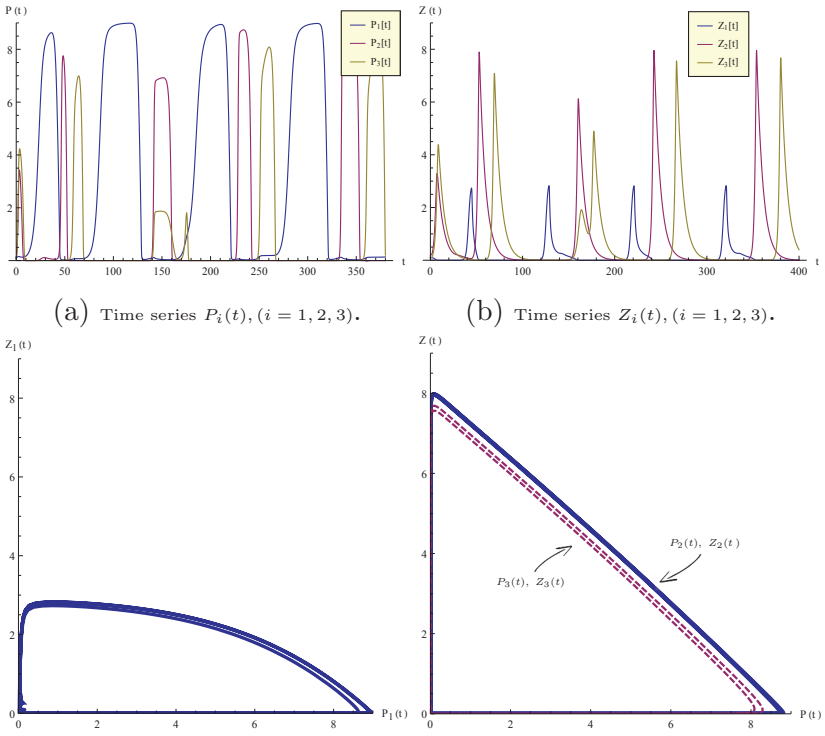
(b) Time series $Z_i(t), (i = 1, 2, 3)$.

(c) $P_1(t)$ and $Z_1(t)$.

(d) $P_i(t)$,$Z_i(t)$, $i = 2, 3$.

$\tau = 0.1,\ P_1(0) = P_2(0) = P_3(0) = Z_1(0) = Z_2(0) = Z_3(0) = 0.1.$

Figure 4.7: (a),(b): Time series $P_i(t)$, $Z_i(t), (i = 1, 2, 3)$; (c), (d): Phase portrait of the system (2.2) with functions and parameters given in (4.4).



(a) Time series $P_i(t), (i = 1, 2, 3)$.

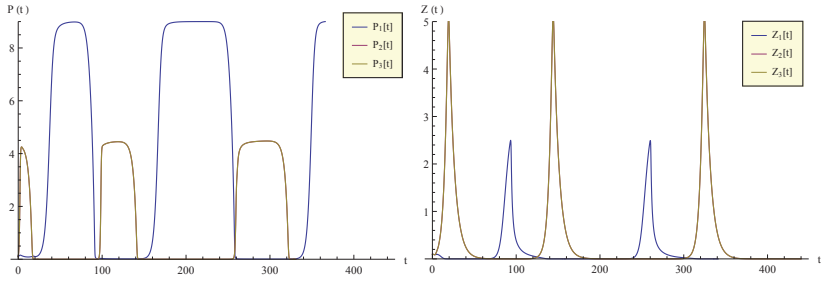
(b) Time series $Z_i(t), (i = 1, 2, 3)$.

(c) $P_1(t)$ and $Z_1(t)$.

(d) $P_i(t)$,$Z_i(t)$, $i = 2, 3$.

$\tau = 0.1,\ P_1(0) = Z_1(0) = 0.1, P_2(0) = 1,\ Z_2(0) = 0.2,\ P_3(0) = Z_3(0) = 0.1.$

Figure 4.8: (a),(b): Time series $P_i(t)$, $Z_i(t), (i = 1, 2, 3)$; (c), (d): Phase portrait of (2.2) with functions and parameters given in (4.4).



(a) Time series $P_i(t), (i = 1, 2, 3)$. (b) Time series $Z_i(t), (i = 1, 2, 3)$.
$\tau = 2.6,\ P_1(0) = P_2(0) = P_3(0) = Z_1(0) = Z_2(0) = Z_3(0) = 0.1.$

Figure 4.9: Time series $P_i(t)$ and $Z_i(t)(i = 1, 2, 3)$ of system (2.2) with functions and parameters given in (4.4).

For the model (3.2) with migration among patches, we provide examples (5-8).

Example 5. When $\tau_1 = \tau_2 = \tau$. We take the functions and the parameters in system (3.3) as,

$$\mu_1(\mathcal{N}) = \mu_2(\mathcal{N}) = \frac{\mathcal{N}}{T},\ h_1(P) = \frac{1}{2P+1},\ h_2(P) = \frac{1}{P+1},\ \epsilon_1(Z) = 0.25,\ \epsilon_2(Z) = 0.3,$$
$$s = 0.9,\ m = 0.1,\ T = 10, d_1 = d_2 = 0.01,\ b_1 = b_2 = 0.25,\ \alpha_1 = \alpha_2 = 1,\ \beta_1 = \beta_2 = 1 \quad (4.5)$$

By Theorem (3.3), we have $\tilde{E} = (5, 0, 5, 0)$ is globally attractive for $\tau > 22.31$. Furthermore, we can check that the condition ($\tilde{\mathbf{H}}_0$), thus $\tilde{E}$ is locally stable at $\tau = 0$. Since $\bar{\tau} = 45.89$ and $0 < A < 1$, $\bar{\bar{\tau}} = 0$, by Theorem (3.4) $\tilde{E}$ is locally stable for $\tau \in (0, 45.89)$, see Fig. (4.10). System (3.3) has two equilibrium points, E_0, $\tilde{E}$, there is no positive point by Lemma (3.1).

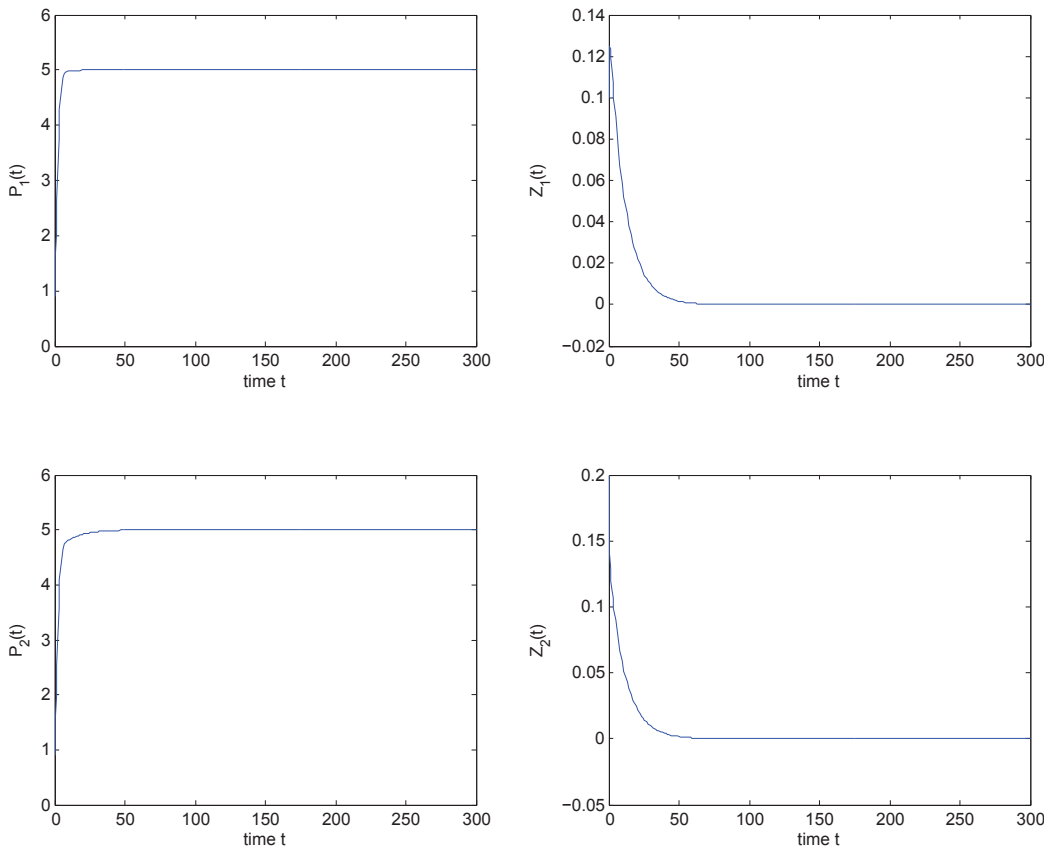
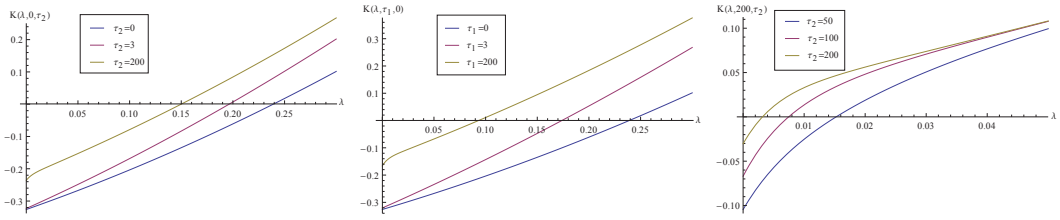


Figure 4.10: Time series $P_i(t)$ and $Z_i(t)$ $(i = 1, 2)$ of system (3.3) with functions and parameters given in (4.5) at $\tau = 0.2$.

Example 6. We take the functions and the parameters in system (3.3) as,

$$\mu_1(\mathcal{N}) = \frac{\mathcal{N}}{1+\mathcal{N}},\ \mu_2(\mathcal{N}) = \frac{\mathcal{N}}{T},\ h_1(P) = \frac{2}{P+3},\ h_2(P) = \frac{1}{P+1},\ \epsilon_1(Z) = 0.01,\ \epsilon_2(Z) = 0.02,$$
$$s = 0.8,\ m = 0.5,\ T = 9, d_1 = d_2 = 0.01,\ b_1 = b_2 = 0.25,\ \alpha_1 = \alpha_2 = 1,\ \beta_1 = \beta_2 = 1. \quad (4.6)$$

First, assume $\tau_1 = 0$. When $\tau_2 = 0$, by checking ($\tilde{\mathbf{H}}_0$), we know $\tilde{E} = (4.5, 0, 4.5, 0)$ is unstable. Fig. (4.11) shows that $K(\lambda, \tau_1, \tau_2) = 0$ has a positive eigenvalue for any



(a) $\tau_1 = 0,\ \tau_2 = 0, 3, 200.$ (b) $\tau_1 = 0, 3, 200,\ \tau_2 = 0.$ (c) $\tau_1 = 50, 100, 200,\ \tau_2 = 200.$

Figure 4.11: Existence of a positive eigenvalue corresponding to the choice in (4.6).

feasible time delay$\tau_1,\ \tau_2 > 0$.

Example 7. We consider a symmetric system with $n = 2$. We take the functions and the parameters in system (3.21) as,

$$\mu(\mathcal{N}) = \frac{\mathcal{N}}{1+\mathcal{N}},\ h(P) = \frac{P}{P^2+1},\ \epsilon(Z) = 0.15,$$
$$s = 0.1,\ m = 0.6,\ T = 8, d = 0.01,\ b = 0.25,\ \alpha = 1,\ \beta = 1. \tag{4.7}$$

System (3.21) has a coexistence equilibrium point $E^* = (P^*, Z^*, P^*, Z^*)$ with

$$\begin{aligned} P^* &= \sqrt{\frac{3}{5e^{-0.01\tau} - 3}}; \\ Z^* &= \frac{9P^* + 2 - \sqrt{16P^{*4} - 64P^{*3} + 97P^{*2} - 28P^* + 4}}{4P^*}, \end{aligned}$$

which is positive If and only if $\tau < 45.02$.

We can check, in this example, $h(P)$ is not a increasing function, from Proposition

(3.3), it's possible to have other positive equilibrium point. However, we have tried different choices of the functions and parameters, we cannot find others except E^*.

At $\tau = 0$, system (3.21) has a stable positive equilibrium is $E^* = (1.225, 1.474, 1.225, 1.474)$. Similarly as in Chapter (2), we can define functions $S_n(\tau)$ $n \in \mathcal{N}$ to find a pure imaginary root for Eq. (3.25). In Fig. (4.12), we plot $S_0(\tau)$, $S_1(\tau)$ and $S_2(\tau)$. We can see that the curve of $S_1(\tau) = 0$ has two roots at $\tau_1^* = 0.41$ and $\tau_2^* = 24.11$. For small delay $\tau < \tau_1^*$, the positive equilibrium point is stable. However, an increase in the delay leads to oscillations and again to a stable positive equilibrium at τ_2^* before it disappears at $\tau = 45.02$. Which implies the occurrence of stability switch. Fig. (4.13) shows time series $P_i(t)$ and $Z_i(t)$, $i = 1, 2$ with different values of τ. Biologically, when the maturation process is too short, the concentration of phytoplankton and zooplankton move to a certain level with constant concentration; while the maturation time increases, all the species oscillate regularly. Nevertheless, a very large maturation age implies that zooplankton stay long in the juvenile phase and take a long time to become active predators. During this time phytoplankton can increase and reach a certain concentration. Which leads to a stable coexistence of zooplankton and phytoplankton again, rather than the oscillation.

Example 8. With n = 2. We take different functional responses and parameters

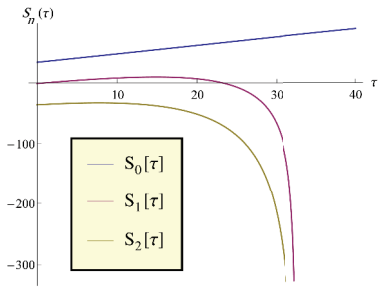
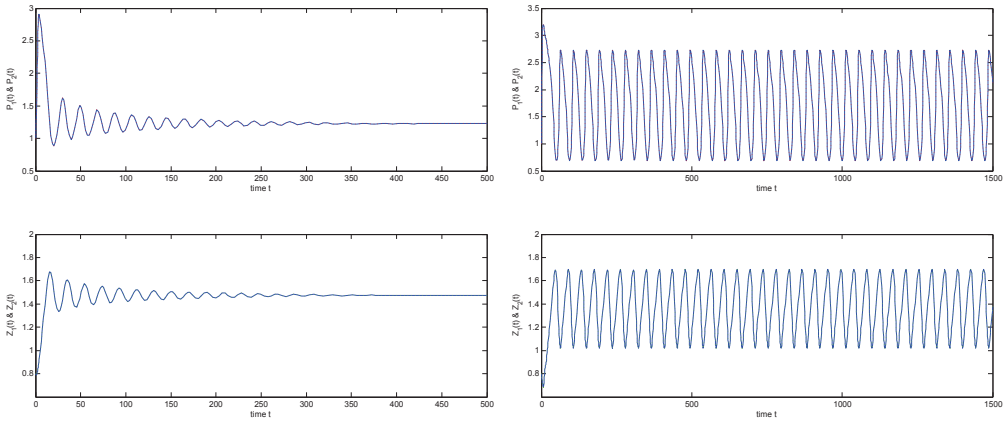


Figure 4.12: Functions $S_0(\tau)$, $S_1(\tau)$ and $S_2(\tau)$ for $\tau \in (0, 45.02)$ corresponding to the choice in (4.7).

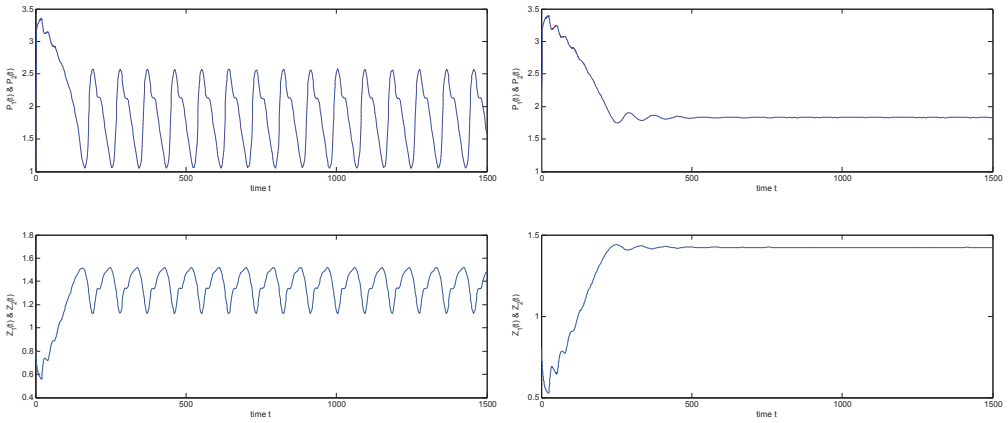
in (3.2), such as,

$$\mu_1(\mathcal{N}) = \frac{T}{\mathcal{N}}, \mu_2(\mathcal{N}) = \frac{\mathcal{N}}{5+\mathcal{N}}, \ h_1(P) = \frac{2}{P+3},$$
$$h_2(P) = \frac{1}{2P+1}, \ \epsilon_1(Z) = 0.1, \ \epsilon_2(Z) = 0.05,$$
$$T = 7, d_1 = d_2 = 0.01, \ b_1 = b_2 = 0.25,$$
$$\alpha_1 = \alpha_2 = 1, \ \beta_1 = \beta_2 = 1, \ s = 0.2, \ \tau_1 = \tau_2 = 0.2. \tag{4.8}$$

In this example, we present how the stability of the positive equilibrium point affected by the prey migration rate m. In Fig. (4.14), we can see that a very small prey migration rate does not affect the system stability. But while the migration rate increase, the system loses its stability.



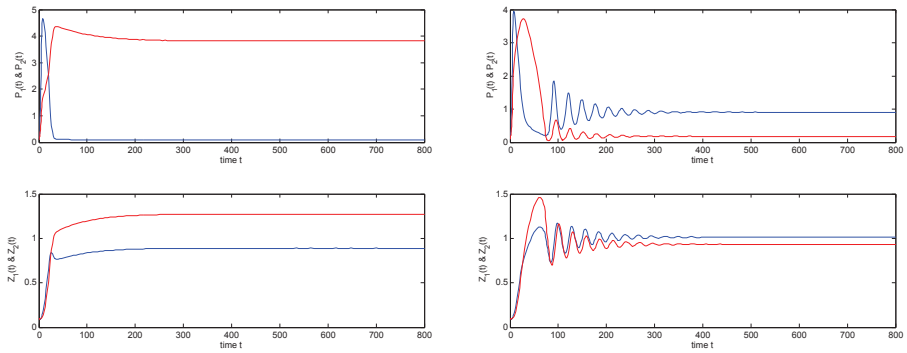
(a) $\tau = 0.25$. (b) $\tau = 7$.



(c) $\tau = 20$. (d) $\tau = 25$.

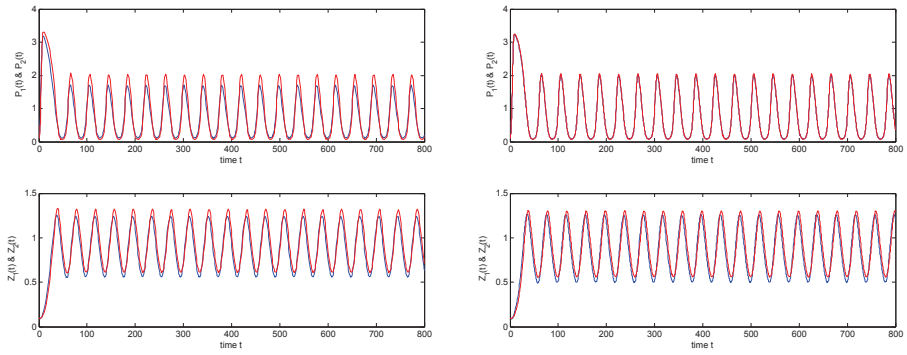
$$P_1(0) = P_2(0) = 1,\ Z_1(0) = Z_2(0) = 0.8.$$

Figure 4.13: Time series $P_i(t)$ and $Z_i(t)$ $(i = 1, 2)$ of system (3.21) with functions and parameters given in (4.7).



(a) $m = 0.01$.

(b) $m = 0.06$.



(c) $m = 0.5$.

(d) $m = 4$.

Figure 4.14: The affection of the prey migration rate in the stability.

Chapter 5

Summary and Future Work

5.1 Research summary

In this thesis, we propose a general model with n parallel food chains through the stage structured maturation time delay. Without migration in Chapter (2), we have carried out mathematical analysis to discuss the existence of the steady states and their stabilities. When $n = 1$, we provide the explicit conditions for the local stability of the one-species or the co-existed species equilibrium points and the global stability of the predator-free equilibrium point. Further, we show that the time delay can, not only destroy the existence, but also destabilize the positive equilibrium even it exists. Later, we extend some of the results for the single patch to the model with $n > 1$

multiple parallel patches.

Then in Chapter (3), we consider interactions between patches and present a more complex model. When $n = 2$, we determine conditions that lead to the predator-free equilibrium point being local stable and global stable when the delays are the same in both patches. For the interior equilibrium points, we are able to provide the explicit conditions for the local stability when all patches are symmetric. Also, we provide some results to the model with $n > 2$.

Finally, to complement the analytical results, we illustrate some numerical simulation to show the rich dynamics in the both systems.

5.2 Future work

Further research of this thesis, one would like to study the influence of the partial symmetry of the system and the possibility to have chaotic motion due to this partial symmetry.

Another direction of future work is in considering the grazing predators which can effect the dynamics of plant populations and communities in marine [KB12], and freshwater [Els92] habitats, one can introduce maturation time delay or a delay in the redistribution of grazing process, Fig. (5.1). Also, one would like to study to study

the effect of adding a stage structure for the prey.

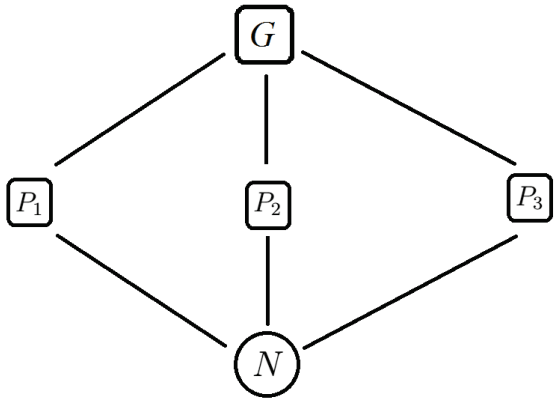


Figure 5.1: Three phytoplankton with a single zooplankton grazers.

Bibliography

[ADY14] I. Al-Darabsah and Y. Yuan. Dynamics of a general stage structured n parallel food chains. *In, Biomat 2013, Proceedings of the International Symposium on Mathematical and Computational Biology, R.P. Mondaini(editor), World Scientific*, pages 63–84, 2014.

[AG89] R. Arditi and L. Ginzburg. Coupling in predator-prey dynamics: Ratio-dependence. *Journal of Theoretical Biology*, 139(3):311–326, 1989.

[AM05] K. Abadir and J. Magnus, editors. *Matrix Algebra*. Cambridge University Press, 2005.

[AP07] R. Mchich P. Auger and J. Poggiale. Effect of predator density dependent dispersal of prey on stability of a predator-prey system. *Mathematical Biosciences*, 206:343–356, 2007.

[Arm99] R.A. Armstrong. Stable model structures for representing biogeochemical diversity and size spectra in plankton communities. *Journal of Plankton research*, 21(3):445–464, 1999.

[BC09] J. Berge and F. Cottier. Diel vertical migration of arctic zooplankton during the polar night. *Biology Letters*, 5:69–72, 2009.

[BK02] E. Beretta and Y. Kuang. Geometric stability switch criteria in delay differential systems with delay dependent parameters. *SIAM J Math Anal.*, 33:1144–1165, 2002.

[CM49] N. Chebotarev and N. Meiman. The routh-hurwitz problem for polynomials and entire functions. *Trudy Mat. Inst. Steklov*, 26:3–331, 1949.

[CN00] X. Zhang L. Chen and A. Neumann. The stage-structured predatorprey model and optimal harvesting policy. *Mathematical Biosciences*, 168:201–210, 2000.

[Col80] C. D. Collins. Formulation and validation of a mathematical model of phytoplankton growth. *Ecology*, 61:639–649, 1980.

[CS82] J. Cushing and M. Saleem. A predator prey model with age structure. *Journal of Mathematical Biology*, 14(2):231–250, 1982.

[CZ11] H. Cheng and T. Zhang. A new predator-prey model with a profitless delay of digestion and impulsive perturbation on the prey. *Applied Mathematics and Computation*, 217:9198–9208, 2011.

[DZ13] F. Wang Y. Kuang C. Ding and S. Zhang. Stability and bifurcation of a stage-structured predatorprey model with both discrete and distributed delays. *Chaos, Solitons & Fractals*, 46:19–27, 2013.

[EB96] A. M. Edwards and J. Brindley. Oscillatory behavior in a three-component plankton population model. *Dynamics and Stability of Systems*, 11(4):347–370, 1996.

[Els92] J. Elser. Phytoplankton dynamics and the role of grazers in castle lake, california. *Ecology*, 73:887–902, 1992.

[EY00] A. M. Edwards and A. Yool. The role of higher predation in plankton population models. *J. Plankton Research*, 22:1085–1112, 2000.

[GK04] S. A. Gourley and Y. Kuang. A stage structured predator-prey model and its dependence on maturation delay and death rate. *J. Math. Biol.*, 49:188–200, 2004.

[HH08] M.D. Holland and A. Hastings. Strong effect of dispersal network structure on ecological dynamics. *Nature*, 456:792–795, 2008.

[Hol59a] C. Holling. The components of predation as revealed by a study of small-mammal predation of the european pine sawfly. *The Canadian Entomologist*, 91(5):293–320, 1959.

[Hol59b] C. Holling. Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist*, 91(7):385–398, 1959.

[Jan94] V. Jansen, editor. *Theoretical Aspects of Metapopulation Dynamcs*. Ph.D. thesis Leiden University The Netherlands, 1994.

[KB12] Julie E. Keister and Delphine Bonnet. Zooplankton population connections, community dynamics, and climate variability. *ICES Journal of Marine Science*, 69(3):347–350, 2012.

[KC82] Z. Grossman K. Cooke. Discrete delay, distributed delay and stability switches. *J. Math. Anal. Appl.*, 86:592–627, 1982.

[KR08] W. Ko and K. Ryu. A qualitative study on general gause-type predator-prey models with constant diffusion rates. *J. Mathematical Analysis and Applications*, 344:217–230, 2008.

[KT94] Y. Kuang and Y. Takeuchi. Predator-prey dynamics in models of prey dispersal in two-patch environments. *Mathematical Biosciences*, 120:77–98, 1994.

[Kua93] Y. Kuang. *Delay Differential Equation with Application in Population Dynamics*. Academic Press, New York, 1993.

[LG81] J Lubchenco and S D Gaines. A unified approach to marine plant-herbivore interactions. i. populations and communities. *Annual Review of Ecology and Systematics*, 12:405–437, 1981.

[LK08] E. Litchman and C.A. Klausmeier. Trait-based community ecology of phytoplankton. *Annu. Rev. Ecol.Evol.Syst.*, 39:615–639, 2008.

[LS10] M.Y. Li and H. Shu. Impact of intracellular delays and target-cell dynamics on in vivo viral infections. *SIAM J. Appl. Math.*, 70(7):2434–2448, 2010.

[ML02] A. Medvinsky S. Petrovskii I. Tikhonova H. Malchowand and B. Li. Spatiotemporal complexity of plankton and fish dynamics. *SIAM Review*, 44:311–370, 2002.

[MN07] W. Michiels and S. Niculescu, editors. *Stability and Stabilization of Time-Delay Systems: An Eigenvalue-Based Approach*. SIAM, 2007.

[Nun85] L. Nunney. The effect of long time delays in predator-prey systems. *Theoretical Population Biology*, 27:202–221, 1985.

[Oll99] K. Olli. Diel vertical migration of phytoplankton and heterotrophic flagellates in the gulf of riga. *Journal of Marine Systems*, 23:145–163, 1999.

[OY09] T. Kolokolnikov C. Ou and Y. Yuan. Phytoplankton depth profiles and their transitions near the critical sinking velocity. *J. Math. Biol.*, 59:105–122, 2009.

[PM07] A. Abdllaoui P. Auger B. Kooi R. Parra and R. Mchich. Effects of density-dependent migrations on stability of a two-patch predator-prey model. *Mathematical Biosciences*, 210:335354, 2007.

[RH11] W. Feng B. Rock and J. Hinson. On a new model of two-patch predator-prey system with migration of both species. *J. Applied Analysis and Computation*, 1:193–203, 2011.

[Sil00] J. R. Silvester. Determinants of block matrices. *Maths Gazette*, 84:460–467, 2000.

[Smi95] H. L. Smith. *Monotone Dynamical Systems: An Introduction to the Theory of Competitive and Cooperative Systems*. American Mathematical Society, 1995.

[Smi10] H. Smith. *An Introduction to Delay Differential Equations with Applications to the Life Sciences*. Springer, 2010.

[WR99] J. Wei and S. Ruan. Stability and bifurcation in a neural network model with two delays. *Physica D*, 130:255–272, 1999.

[Yua12] Y. Yuan. A coupled plankton system with instantaneous and delayed predation. *J. Biological Dynamics*, 6:148–165, 2012.